
Emotional Egocentricity in Development and Psychopathology

Emotional Egocentricity in Development and Psychopathology

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1. Theoretical and Empirical Background

1.1 Routes towards the understanding of other minds

It has always been a great puzzle to us how we can understand the minds of other people and accurately predict their behaviour, especially as we lack any privileged access to other minds as we have to our own. Many great thinkers in history have attempted to answer this question, proposing different solutions (Hume, 1739/1978; Lipps, 1903; Merleau-Ponty, 1962), but till now, reaching into the contemporary debate, the puzzle is far from solved. Nowadays it is commonly considered that in social cognition there exist two main routes towards understanding the other's inner world (Frith & Frith, 2012; Shamay-Tsoory, 2011; Singer, 2006, 2012). On the one hand there exists a cognitive route often termed Theory of Mind (ToM), which represents the ability to understand the mental states of others, such as beliefs and intentions (Premack & Woodruff, 1978), and on the other hand there the affective route in empathy, which represents the ability to understand and share feelings of others (Batson, 2009; Eisenberg, 2000; Singer, 2012; Singer & Lamm, 2009; Singer et al., 2004). Both processes have been linked to diverging networks within the human brain (Figure 1.1).

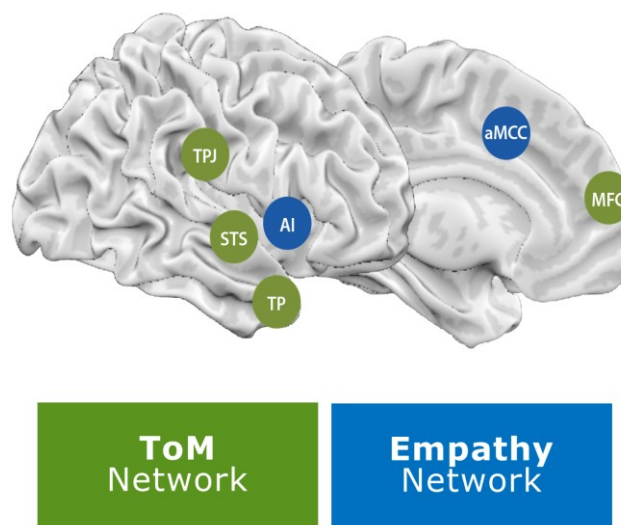


Figure 1.1. Schematic depiction of the Theory of Mind (ToM) network and the empathy network.

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Neuroimaging studies have shown that Theory of Mind involves a particular set of brain regions such as the medial prefrontal cortex (MPFC), the precuneus and posterior cingulate cortex (PCC), right and left temporo parietal junction (r/ITPJ), and bilateral temporal poles (Aichhorn, Perner, Kronbichler, Staffen, & Ladurner, 2006; Frith & Frith, 2006; Saxe & Kanwisher, 2003; Van Overwalle, 2009), whereas empathy relies on another set of brain regions, such as the bilateral insulae, and the middle cingulate cortex (MCC, Lamm, Decety, & Singer, 2011; Singer et al., 2004). Besides these two routes there is a potential third route towards understanding the other in social cognition. This research is based around the discovery of the “mirror neuron system” (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996), which describes a particular set of neurons in the monkey and human brain that tend to respond when a goal-directed action is observed by an agent, as well as when the agent performs the goal-directed action him/herself. The mirror neuron system has potential implications for imitation and our ability to represent goals and intentions of others, while possibly representing a basis for higher order routes of social cognition such as aforementioned ToM and empathy (Gallese & Goldman, 1998). Within the human brain the mirror neuron systems is assumed to be comprised of the inferior parietal lobule (IPL), ventral premotor cortex, and the caudal part of the inferior frontal gyrus (IFG, Blakemore & Decety, 2001; Dinstein, Hasson, Rubin, & Heeger, 2007; Etzel, Gazzola, & Keysers, 2008; Gazzola, Aziz-Zadeh, & Keysers, 2006). It has to be noticed that the exact functional role of the mirror neuron system remains elusive, and that whether mirror neurons really code for intentions of agents is still a topic of debate (Cook, Bird, Catmur, Press, & Heyes, 2014; Csibra & Gergely, 2007; Heyes, 2010). The existence of mirror neurons has been commonly interpreted as a support for ‘simulation accounts’ (Gallese, 2001; Gallese & Goldman, 1998), which broadly suggest that other people’s actions, sensations and feelings are understood via activations of the neural representations corresponding to these states. For ToM as well as empathy the processes of simulation and projection have been suggested as crucial mechanisms to understand the inner

world of another person (e.g. Gallese, 2001; Gallese & Goldman, 1998; Mitchell, 2009; Nickerson, 2001; Silani, Lamm, Ruff, & Singer, 2013; Van Boven & Loewenstein, 2003). These simulation accounts of ToM and empathy have been most strongly supported by findings showing that shared neural activations between self and other underlie our ability to represent the internal states of others (Mitchell, 2009; Singer et al., 2004). It has to be noted here however that simulation and projection might be by no means the exclusive mechanisms towards understanding other minds, as different theoretical propositions have been made and are still debated, which also do not have to be considered mutually exclusive (Bohl & van den Bos, 2012; Gallagher, 2001; Saxe, 2005).

1.2 When simulation fails and egocentricity arises

While simulation and projection represent fundamental mechanisms in social cognition towards understanding other minds, they can become inefficient as soon as one's own mental state or internal experience differs to that of another person. For instance it would be erroneous to assume someone was happy while he clearly is sad just because we ourselves feel happy. The tendency to project one's own mental states onto others has been broadly termed as egocentricity bias.

In the domain of ToM egocentricity has been commonly reported and findings show that egocentricity can even be detected in healthy adults (Pronin, 2008; Royzman, Cassidy, & Baron, 2003). Exemplary for such a “cognitive egocentricity” in ToM, has been reasoning about false beliefs, during which a person A has to detach from his/her true belief about an object X to consider the false belief of a person B about object X. In such a circumstance a simple simulation mechanism would fail to accurately make sense of another persons' incongruent mental state (false belief in this case) and lead to egocentrically biased

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judgments. To avoid such egocentrically biased judgments, a self-other distinction mechanism differentiating between self and other perspectives must be in place. This so called self-other distinction has been proposed to play a key role in social cognitive processes (Brass, Ruby, & Spengler, 2009; Decety & Sommerville, 2003; Meltzoff & Decety, 2003; Santiesteban, White, et al., 2012). A key brain region that seems adequately suited for distinguishing and switching between self and other perspectives in the cognitive domain, being a hub of both interoceptive and exteroceptive information pathways is the so-called temporo-parietal junction (TPJ). TPJ has shown to be consistently recruited during belief reasoning and perspective-taking (Aichhorn et al., 2006; Decety & Lamm, 2007; Ramsey, Hansen, Apperly, & Samson, 2013; Sommer et al., 2007). In particular the right TPJ, has been suggested to play a major role during ToM (Saxe & Kanwisher, 2003), especially when a difference in perspective exists between self and other (Aichhorn et al., 2006; Sommer et al., 2007). Furthermore it has however been proposed that rTPJ plays a much more general role in self-other distinction which extends from the cognitive into the motor domain. Results from meta analyses (Bzdok et al., 2013; Decety & Lamm, 2007; Silani et al., 2013) and also single studies showed a relation between the inhibition of spontaneous imitation tendencies (i.e. self-other distinction in the motor domain) and ToM abilities (Santiesteban, White, et al., 2012; Spengler, von Cramon, & Brass, 2009, 2010). Strong evidence comes from a recent study using transcranial direct current stimulation (tDCS) of rTPJ showing that rTPJ is causally involved in differentiating self and other representations during imitation inhibition and cognitive perspective-taking (Santiesteban, Banissy, Catmur, & Bird, 2012). Thus findings so far suggest that rTPJ functioning might be crucial in differentiating self and other perspectives in the cognitive domain, and therefore subsequently in helping to overcome cognitive egocentricity during ToM.

In the domain of empathy, egocentricity has not been investigated until recently. Some initial studies have however looked at egocentricity during attributing visceral states (Van

Boven & Loewenstein, 2003). In previous empathy studies emotional states of the person who empathizes and the person suffering were never incongruent (Singer et al., 2004; Singer et al., 2006). However this does not seem likely and representative of everyday life, where the constant ebbing and flowing of thoughts and feelings permits perfect alignment of individual minds. Thus overcoming emotional egocentricity during empathic judgments might be of similar importance to overcoming egocentricity during ToM reasoning, to eventually arrive at an accurate understanding of another person's mental state. A study by Silani et al. (2013) recently demonstrated that healthy adults show an emotional egocentricity bias (EEB) when judging the emotional state of another person that was incongruent to their own, while the right supramarginal gyrus (rSMG) was functionally implicated in overcoming emotional egocentricity. Peaks of this activation were distinct from other subregions of temporo-parietal cortex involved in ToM. The specific role of rSMG in overcoming EEB and thus self-other distinction in the affective domain was buttressed by findings of an increased EEB when disrupting rSMG with repetitive transcranial magnetic stimulation. In line with these findings, a study by Steinbeis, Bernhardt, and Singer (2014) showed that children displayed increased emotional egocentricity compared to adults related to reduced activation of rSMG. In a complementary resting-state connectivity analysis rSMG stronger functional connectivity to regions of the empathy network, such as the MCC and bilateral anterior insulae (AI), extending to inferior frontal gyrus (IFG) and bilateral dorsolateral prefrontal cortex (DLPFC), while rTPJ showed stronger functional connectivity to nodes of the ToM network, including the medial prefrontal cortex (MPFC) and the precuneus. Taken together these findings corroborate the hypothesis that the broader area usually referred to as temporal parietal cortex consists of important subdivisions that in turn might subserve different functions in the context of social cognition respectively. Within the affective route towards understanding the other, rSMG seems to be implicated in overcoming emotional egocentricity, whereas within

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the cognitive route of ToM, rTPJ seems to play an important role in overcoming cognitive egocentricity (Figure 1.2).

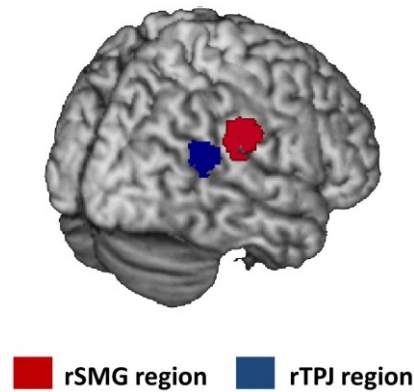


Figure 1.2. The rSMG region depicted consists of an overlap of activations of two fMRI experiments looking at the neuronal basis of the EEB using the ETOP (Silani et al., 2013). The rTPJ region was taken from a meta-analytic activation during ToM (Mar, 2011).

Increased cognitive egocentricity has been a particularly striking phenomenon in children and various mental disorders, leading to a wealth of scientific investigation there of. In contrast emotional egocentricity has so far not been adequately addressed in previous research, despite being of equal importance in regards to social cognition in children and adult psychopathologies. This dissertation thus represents an attempt to answer relevant questions about emotional egocentricity and its causes in child development and adult psychopathology. In the subsequent parts a short overview will be given about what is presently known about egocentricity in the domain of child development and in the domain of adult psychopathology, with the specific focus for the latter on Autism Spectrum Disorder (ASD) and Major Depressive Disorder (MDD).

1.3 Egocentricity in child development

Egocentricity in child development has been a commonly reported phenomenon (Elkind, 1967; Flavell, 1999; Kohlberg, 1976; Piaget & Inhelder, 1956). The term egocentrism in developmental psychology originates most prominently from the work of Jean Piaget, in which each of his developmental stages of cognitive development has been associated with its unique egocentrism to be overcome. Equally influential has been Kohlberg's work on children's egocentrism during moral development (Kohlberg, 1976). Kohlberg showed that children from 2 to 9 tended to solve moral scenarios mostly from an egocentric perspective, reasoning morally particularly when it benefited the self (Kohlberg, 1976). Egocentricity during visual perspective taking has been investigated by Piaget & Inhelder (1956), with the famous "three mountains" task, in which children at the age of 7 exhibit difficulties judging someone else's visual perspective which differs from their own. Subsequent research has thus focused predominantly on investigating developmental egocentricity in children in the domain of social cognition using visual perspective taking and ToM tasks (Birch & Bloom, 2007; Flavell, Everett, Croft, & Flavell, 1981; Pronin, 2008; Royzman et al., 2003; Thomas & Jacoby, 2012). Children generally exhibit stronger egocentricity during visual perspective taking and Theory of Mind tasks than adults. Before the age of 4 children have difficulties attributing false beliefs to other people, unable to detach from their own true beliefs, leading to egocentrically biased judgments (Wimmer & Perner, 1983). Also, throughout childhood difficulties in visual perspective taking and Theory of Mind (ToM) seem to persist (Apperly, Warren, Andrews, Grant, & Todd, 2011; Keysar, Lin, & Barr, 2003; Sommerville, Bernstein, & Meltzoff, 2013).

While strong evidence for egocentricity in the cognitive domain in children as well as adults has accumulated over the past decades, very little research focused on investigating egocentricity in the affective domain (see O'Brien & Ellsworth, 2012; Repacholi & Gopnik, 1997; Silani et al., 2013; Van Boven & Loewenstein, 2003) and only one study has so far

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looked specifically at emotional egocentricity and its neural correlates in children (Steinbeis et al., 2014). The findings of this study showed that children between the ages of 6 and 12 displayed increased emotional egocentricity compared to adults which was related to reduced activation of rSMG in the brain as well as reduced coupling between rSMG and DLPFC. These findings provided evidence for the neural correlates of increased emotional egocentricity in children, however the exact underlying mechanisms of age-related differences in emotional egocentricity still remain to be identified.

1.4 Egocentricity in adult psychopathology

Many psychological disorders are known to have profound disturbances in social functioning (Brüne & Brüne-Cohrs, 2006; Decety & Meyer, 2008). Egocentrism and self-centeredness during social functioning are among the most common symptoms for a wide range of psychopathologies (Baron-Cohen, Leslie, & Frith, 1985; Blair, Peschardt, Budhani, Mitchell, & Pine, 2006; Brüne, 2005; Taber-Thomas et al., 2014; Wolkenstein, Schönenberg, Schirm, & Hautzinger, 2011). In the following sections Autism Spectrum Disorder (ASD) and Major Depressive Disorder (MDD) will be introduced, with the focus on the specific characteristics of social cognition deficits in these disorders.

1.4.1 Autism Spectrum Disorder (ASD)

ASD is a common, early-onset neurodevelopmental disorder characterized by impairments in social communication, interaction, and stereotyped or repetitive behaviours and interests (American Psychiatric Association, 2013). Some of the social deficits in ASD, as the term ‘autism’ (from ‘autos’, greek for self) suggests, have been linked to an unusual egocentrism. Already in his original paper Asperger (1944) described the children he studied as being

“egocentric to the extreme”. Consequently, one of the most consistently reported social cognition deficits in ASD has been in Theory of Mind (ToM, Baron-Cohen et al., 1985; Castelli, Frith, Happé, & Frith, 2002; Frith & Frith, 2012; Happé, 1994). When engaging in ToM tasks, egocentrism of individuals with ASD is for example evidenced by their increased difficulty in passing false belief tasks (Baron-Cohen et al., 1985; Begeer, Bernstein, van Wijhe, Scheeren, & Koot, 2012; Schneider, Slaughter, Bayliss, & Dux, 2013; Senju et al., 2010; Senju, Southgate, White, & Frith, 2009). It has been proposed that the underlying problem in ToM and in particular false belief understanding for individuals with ASD are difficulties in differentiating between representations of one’s own mental state and that of others, also known as self-other distinction (Lombardo & Baron-Cohen, 2011). Adding support to this notion TPJ, which has been implicated in self-other distinction as mentioned above has been shown to be structurally and functionally abnormal in ASD and linked to social deficits (Castelli et al., 2002; David et al., 2013; Kana, Libero, Hu, Deshpande, & Colburn, 2012; Lombardo, Chakrabarti, Bullmore, & Baron-Cohen, 2011; Mueller et al., 2013; Pitskel, Bolling, Hudac, et al., 2011; Washington et al., 2013). Whether empathy, representing the affective route towards understanding other minds is deficient in ASD remains still a point of debate (Bird & Cook, 2013; Bird et al., 2010; Hadjikhani et al., 2014). Some findings however suggest that social deficits in ASD are much less pronounced in the affective domain. For example there is evidence that individuals with ASD might show intact empathy (Bird et al., 2010; Dziobek et al., 2008; Jones, Happé, Gilbert, Burnett, & Viding, 2010; Lockwood, Bird, Bridge, & Viding, 2013) and if they show empathic deficits, that these might rather relate to the comorbidity of alexithymia than to the diagnosis of ASD itself (e.g. Bird et al., 2010; Silani et al., 2008). Alexithymia is characterized by difficulties in identifying and describing one’s own emotional state (Sifneos, 1973), and has been shown to be normally distributed in the general population (Franz et al., 2008). It has been found that individuals with high alexithymic traits do show deficits in empathy and emotional

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awareness, which among other brain regions is linked to deficits in AI functioning (Bird et al., 2010; Moriguchi et al., 2007; Silani et al., 2008). Whether egocentrism in ASD extends from the cognitive domain of ToM further into the affective domain of empathy, has yet to be investigated.

Another mental disorder having been described to show blatant egocentrism in social cognition is Major Depressive Disorder, which is discussed in more detail in the next section.

1.4.2 Major Depressive Disorder (MDD)

MDD has been characterized by increased negative self-focused thoughts, as well as apathy and social withdrawal (American Psychiatric Association, Association, 2013), and is sometimes described as a disorder of the self (Northoff, 2007). Thus, impairments in social functioning are often reported (Hirschfeld et al., 2000). However, the exact nature of social cognition deficits MDD still remains elusive. Some studies using subjective as well as objective measures do suggest that MDD patients do show cognitive egocentricity during ToM reasoning (Inoue, Tonooka, Yamada, & Kanba, 2004; Schreiter & Pijnenborg, 2013; Wolkenstein et al., 2011; Zobel et al., 2010). Other findings suggest no difference in ToM reasoning between MDD patients and healthy controls (Schreiter & Pijnenborg, 2013; Thoma et al., 2011; Wilbertz, Brakemeier, Zobel, Härter, & Schramm, 2010). These mixed results might have been due to not having accounted for executive functions in depression, which do play an important part in more complex ToM reasoning (Thoma et al., 2011; Zobel et al., 2010). Similarly within the domain of empathy, mixed results have been reported, with the greatest consensus on heightened personal distress (Schreiter & Pijnenborg, 2013), the self-oriented, aversive emotional reaction, such as anxiety or discomfort, towards another person's emotional state (Davis, 1980). With regards to empathy deficits in depression, similarly to the case of autism, the role of alexithymia, a common comorbid personality trait in depression

(Honkalampi, Hintikka, Tanskanen, Lehtonen, & Viinamäki, 2000; Taylor & Bagby, 2004), has to be closely considered. Thus, empathy deficits in depression may well be associated with alexithymia, but further research is needed for clarification. While empathic deficits could relate to comorbid alexithymia in depression, it remains totally unclear whether individuals with depression show increased egocentric bias during empathic relating, when emotional perspectives of self and other differ, and how this would be affected by concurrent alexithymia.

In the next sections the different research questions that motivated the three studies of the present dissertation will be introduced and discussed.

1.5 Research questions

1.5.1 Why do children show increased emotional egocentricity?

Prior work has shown that children display increased emotional egocentricity compared to adults and provided a coherent account of the neural mechanisms leading to this developmental change (Steinbeis et al., 2014). What is still missing and has not been addressed in previous research, is a systematic analysis of the exact cognitive and affective mechanisms that may account for observed age-related differences in emotional egocentricity during development. This question was addressed in study 1 using a newly developed paradigm based on visuo-gustatory stimulation, the EEB Taste-Paradigm (ETAP). During the ETAP participants are asked to judge the pleasantness of their own taste experiences or that of another person, while both can have congruent or incongruent taste experiences. Pilot work indicated that gustatory stimulation elicits equal feelings of pleasantness and unpleasantness in children and adults, making it highly suited to study developmental differences in EEB as

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well as extending the phenomenon of EEB to another stimulus modality. As in the previous study (Steinbeis et al., 2014), it was expected that children would show an increased EEB compared to adults, which would decrease with age. As overcoming such EEB presumably relies on a multitude of higher- and lower-level cognitive and affective processes, we aimed to comprehensively test for these possible processes underlying the developmental differences in EEB using a large battery of tasks. Among those processes tested in relation to emotional egocentricity, were processing speed, attentional reorienting, response inhibition, visual perspective taking, emotion regulation and conflict processing. The findings of Steinbeis et al. (2014) already showed that children's increased emotional egocentricity could not be explained by abilities in response inhibition, attentional reorienting or ToM reasoning. However to replicate these results in this study measuring emotional egocentricity using the ETAP, a response inhibition and attentional reorienting task were again included. Cognitive egocentricity was measured with a visual perspective-taking task that was much closer in design to the ETAP than the previously used ToM reasoning task, varying the congruency of self and other perspectives. Based on Steinbeis et al. (2014), some prime candidates were of particular interest in explaining increased emotional egocentricity in children, namely conflict processing and emotion regulation. While the DLPFC is crucially involved in overcoming emotional egocentricity it also plays an important role in conflict processing as well as emotion regulation (Badre & Wagner, 2004; Egner, Etkin, Gale, & Hirsch, 2008; Egner & Hirsch, 2005; Lévesque et al., 2003), two abilities which show considerable change over development (Fjell et al., 2012; McRae et al., 2012; Pitskel, Bolling, Kaiser, Crowley, & Pelphrey, 2011). The DLPFC is also a part of the brain that is commonly known to mature rather late in development (Gogtay et al., 2004; Steinbeis, Bernhardt, & Singer, 2012).

In sum study 1 aimed to investigate the underlying mechanism of increased emotional egocentricity in children and to explore whether emotional egocentricity and cognitive egocentricity would be interrelated in child development.

1.5.2 Is there increased emotional egocentricity in Autism Spectrum Disorder?

While increased cognitive egocentricity in ASD based on deficits in ToM and its underlying neuronal network has been frequently reported it remains so far unclear whether excessive egocentricity also extend to difficulties in distinguishing self and other perspectives during empathy. In other words, whether egocentrism in ASD is as “extreme” as Asperger envisioned. Recent research provided initial evidence that there may be functionally distinct neural circuits subserving the capacity to overcome cognitive as compared to emotional egocentricity (Silani et al., 2013; Steinbeis et al., 2014). These findings corroborate the hypothesis that the broader area usually referred to as temporal parietal cortex consists of important subdivisions that in turn might subserve different functions in the context of social cognition respectively such as self-other distinction during empathic relating on the one hand as compared to self-other distinction during ToM. It therefore remains an open question whether individuals with ASD show egocentricity across the cognitive as well as the affective domains. The aforementioned findings indicate that overcoming emotional egocentricity might be independent of overcoming cognitive egocentricity relying crucially on rSMG function rather than rTPJ function. This could suggest that individuals with ASD might show intact self-other distinction during empathic relating, reflected in an EEB comparable in size to healthy controls.

The first aim of study 2 was to investigate behaviourally whether individuals with ASD compared to matched healthy controls would show intact self-other distinction during empathic relating, thus normal emotional egocentricity as measured through the EEB Touch-Paradigm (ETOP, Silani et al., 2013). In addition ToM abilities were investigated with an established ToM task, to replicated findings of deficient ToM in ASD. During the ETOP participants are asked to judge the pleasantness of their own tactile experiences or that of another person, while both can have congruent or incongruent tactile experiences. The second aim of study 2 was to test for differences in the associated brain regions supporting these

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functions. In order to do so resting-state functional connectivity data seeding from rTPJ, a brain region commonly implicated in ToM and rSMG, a brain region implicated in self-other distinction during empathy, respectively was analyzed in an independent large multi-center sample of individuals with ASD and matched healthy controls.

In sum in study 2 it was explored whether individuals with ASD relative to healthy controls would in the affective domain show normal emotional egocentricity, differentiating self and other perspective during empathic relating, associated with intact functioning of the rSMG-related brain network. In addition it was hypothesized that individuals with ASD relative to healthy controls would exhibit known deficits in ToM possibly based on problems differentiating self and other perspectives in the cognitive domain related to aberrant functioning of the rTPJ-related brain network.

1.5.3 Egocentric and altercentric biases during empathic relating in Major Depressive Disorder and the role of alexithymia

As mentioned before, findings of empathic deficits in depression have been mixed so far, with the greatest consensus on heightened personal distress (Schreier & Pijnenborg, 2013). This lack of clear evidence for empathy deficits in depression may be related to the fact, that alexithymia has commonly not been accounted for and that emotional states of self and other during empathy tasks have never been varied, mirroring more complex everyday empathic relating. Thus, in study 3 we aimed to arrive at a more comprehensive picture of empathic relating in depression, elucidating the role of alexithymia while looking at empathic relating under simple and complex conditions using the ETOP, manipulating the congruency of emotional perspectives of self and other. Findings of deficient emotion regulation abilities (Berpohl et al., 2009; Joormann & Gotlib, 2010; Kanske, Heissler, Schönfelder, & Wessa, 2012), heightened processing of negative stimuli (Leppänen, 2006; Sterzer, Hilgenfeldt, Freudenberg, Berpohl, & Adli, 2011) and deficient emotional and non-emotional emotional

conflict processing (Etkin & Schatzberg, 2011; Kanske & Kotz, 2012; F. Murphy et al., 1999; Paelecke-Habermann, Pohl, & Lepow, 2005; Waring, Etkin, Hallmayer, & O'Hara, 2013) could suggest that individuals with depression, even if they possess intact simulation under simple empathy conditions, when emotional perspectives between self and other do not differ, might show increased egocentric bias under more complex empathy conditions, when needing to detach from their own emotional perspective to take the incongruent emotional perspective of another person. Emotional judgments of one's own emotional perspective can however also be influenced by another persons' emotional perspective, leading to an altercentric bias. Such an altercentric bias represents a form of emotional contagion, the automatic and implicit tendency to resonate and be affected by another person's emotional perspective (Singer & Lamm, 2009). To investigate the altercentric bias during empathic self judgments in depression, is of interest as for example heightened personal distress is commonly reported in depression (Schreier & Pijnenborg, 2013), suggesting that individuals with depression might also have difficulties detaching emotional perspectives of others from their own, showing heightened emotional contagion.

Alexithymia has been shown to decrease empathic relating based on simulation in healthy controls and also in ASD (Bird & Cook, 2013; Bird et al., 2010), and thus will also most likely in depression. How alexithymia however affects empathic relating under complex conditions in healthy controls as well as in depression remains totally unknown. It could be suggested that individuals with alexithymia would experience diminished emotional conflict due to diminished emotional awareness, finding it easier to detach from their own emotional perspective during empathic relating, leading to a decreased egocentric bias. Emotional contagion on the other hand, being a largely unconscious process, might be less affected by alexithymia.

In sum we hypothesized in study 3 that if simulation processes are intact in depression, depressed patients might show normal empathic relating under simple conditions, when

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alexithymia is controlled for. We also expected individuals with depression to have particular problems in resolving conflicting emotional perspectives, thus suggesting increased egocentric and altercentric biases relative to healthy controls, during empathic relating under complex conditions. Alexithymia was hypothesized to influence the size of the egocentric bias during empathic relating, as less emotional awareness should decrease the emotional conflict between the different perspectives. In contrast, we expected that alexithymia would have less of an influence on the altercentric bias, as emotional contagion should not be affected that much by emotional awareness.

1.6 Method: Emotional Egocentricity Paradigms

In all three studies emotional egocentricity in participants was assessed using emotional egocentricity paradigms. In study 1 the newly developed EEB Taste-Paradigm (ETAP) based on gustatory stimulation was used. In study 2 and 3 emotional egocentricity was assessed with the established EEB Touch-Paradigm (ETOP, Silani et al., 2013) based on tactile stimulation. In the next part the basic setup and procedure of these emotional egocentricity paradigms will be introduced in detail, as they represent the essential methodology that connects all the three studies presented in this dissertation. The other tasks which varied across studies will be described in detail in each of the manuscript sections (see Chapters 2-4).

During the emotional egocentricity paradigms participants are seated back to back in front of a touch screen unable to see the other person's face and emotion judgments. This means that any influence of the other participant's actual emotional state can not have any influence on ratings, as the emotion judgment is exclusively made through the visual cue of what the other was currently experiencing. Before the start of the experiment participants are familiarized with the rating scale and perform 10 practice trials for each condition.

Participants start with the individual conditions in which they are instructed to either judge the pleasantness of their gustatory or tactile experience or judge the pleasantness of the gustatory or tactile experience for the other person (blocked design). In the case of the ETAP pleasant and unpleasant gustatory stimuli (e.g. juices, bitter solutions) are being presented to the participants by a custom-built pump-system specifically designed for this study via several small plastic tubes, which merge together at the end into a mouthpiece with small bundled tubes (for more detail see Chapter 2). In the case of the ETOP, the participant's hand is being touched by different objects, eliciting pleasant and unpleasant tactile experiences (e.g., silk, rubber spider, for more detail see Chapters 3 and 4). In the individual self condition, a picture corresponding to the specific tactile or gustatory stimuli (i.e. a picture of a glass of orange juice when the participant received orange juice) appears on the screen and remains there until the end of the gustatory or tactile stimulation which lasts 1500 ms for the ETAP and 3000 ms for the ETOP. In the case of the ETAP the corresponding picture of the gustatory stimuli appeared already 500 ms before the stimulation to prepare the participants a little bit in advance. Immediately after the end of the stimulation phase participants have to judge the experienced pleasantness or unpleasantness of the gustatory or tactile experience by using a rating scale (ranging from -10 to +10) on the touch screen, within a 1500 ms response time for the ETAP and a 3500 ms and 2000 ms response time for the ETOP in study 1 and study 2. In case of the ETAP after the emotion judgment a picture with a water drop appears on the screen and water is pumped simultaneously through a tube for a rinse. The rinse lasts for 2000 ms followed by an instruction to swallow (1000 ms) and a fixation cross (2000 ms). In the individual other condition, the trial structure remains the same for the ETAP as well as ETOP, but with the important difference that the participant does not receive gustatory or tactile stimuli and is instead instructed to judge the pleasantness or unpleasantness of the gustatory or tactile experience for the other participant also present in the room based on the picture which indicates what gustatory or tactile stimuli the other person receives. Each run consists

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of 30 pseudo-randomized trials, with 10 pleasant, 10 neutral and 10 unpleasant visuo-gustatory or visuo-tactile stimuli.

The individual conditions are followed by the simultaneous conditions (trial example for the ETAP, see Figure 1.3).

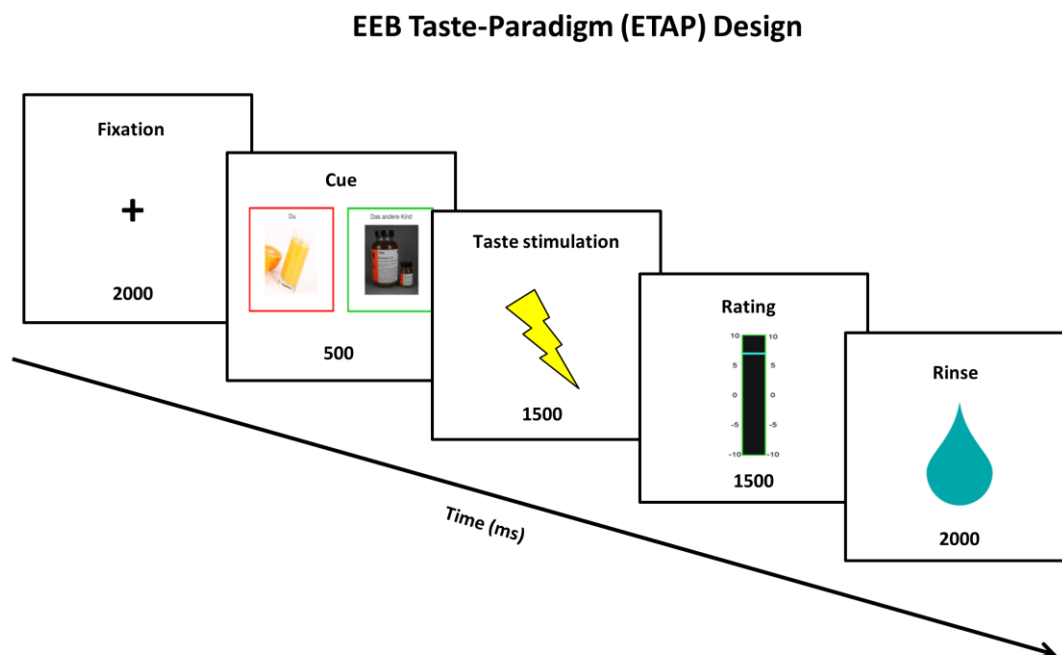


Figure 1.3. EEB Taste-Paradigm (ETAP) design: Trial structure of the simultaneous other condition.

In these simultaneous conditions both participants in the room receive gustatory or tactile stimuli simultaneously, and are instructed to either judge the pleasantness of their own or tactile gustatory experience (simultaneous self condition) or judge the pleasantness of the gustatory or tactile experience for the other person (simultaneous other condition). The simultaneous self and simultaneous other conditions are blocked and counterbalanced. In these conditions two pictures appear on the screen. The left picture is labelled “Self” on the top and corresponded to the gustatory or tactile stimulation the participant receives, while the right picture labelled “Other” corresponds to the gustatory or tactile stimulation the other person receives. The gustatory or tactile experiences of the two participants can be either

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affectively congruent (e.g. both receive positive gustatory or tactile stimuli) or incongruent (e.g. one receives positive, the other negative gustatory or tactile stimuli). The EEB is defined as the difference between ratings in incongruent and congruent trials when judging the other, as compared to the difference when judging one's own feelings (see Figure 1.4 and Figure 1.5 experimental designs of the ETAP and the ETOP).

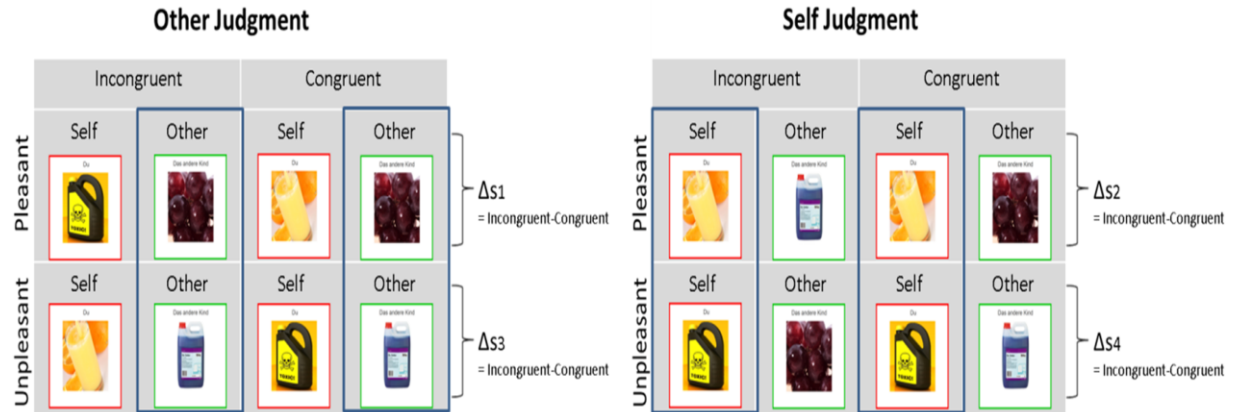


Figure 1.4. Experimental design of the ETAP with the factors target (self/other judgment), valence (pleasant/unpleasant), and congruency (incongruent/congruent). The EEB is calculated as follows:

$$EEB = [-1 * (\Delta s1 - \Delta s2) - (\Delta s3 - \Delta s4)] / 2.$$

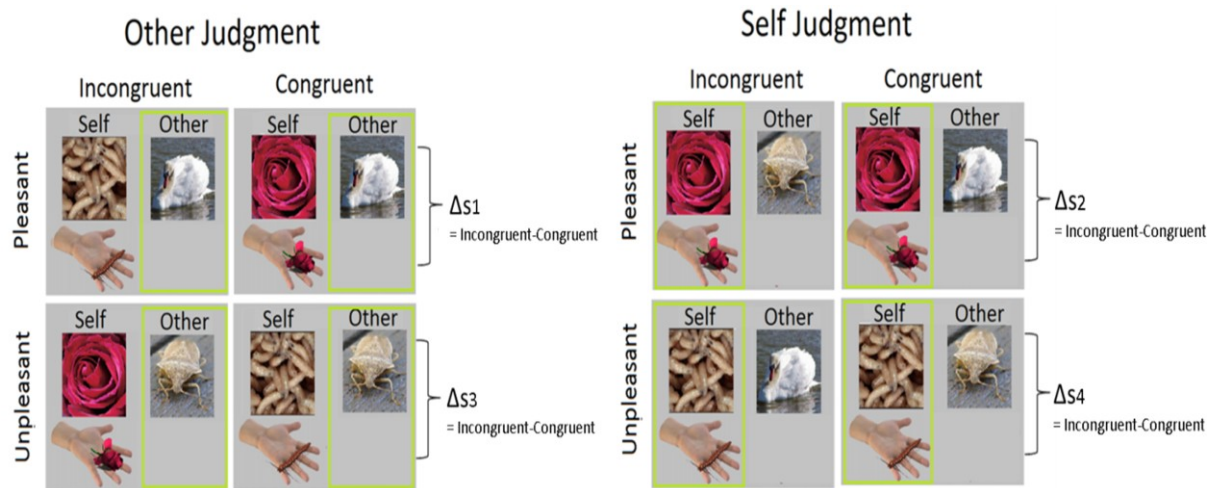


Figure 1.5. Experimental design of the ETOP with the factors target (self/other judgment), valence (pleasant/unpleasant), and congruency (incongruent/congruent). The EEB is calculated as follows:

$$EEB = [-1 * (\Delta s1 - \Delta s2) - (\Delta s3 - \Delta s4)] / 2.$$

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In the simultaneous conditions for adults each run consists of 40 pseudo-randomized trials, with 20 pleasant (10 congruent and 10 incongruent) and 20 unpleasant (10 congruent and 10 incongruent) visuo-gustatory or visuo-tactile stimuli. Simultaneous conditions are blocked according to target, so that half the participants start with the self judgment and half of the participants starts with the other judgment.

1.7 Summary of the main findings

1.7.1 Study 1

Study 1 investigated the underlying mechanism of increased emotional egocentricity in children between the ages of 7 to 12 compared to adults, by using the newly designed ETAP based on visuo-gustatory stimulation, while also assessing various socio-cognitive and socio-affective functions. As compared to previous studies using either a visuo-touch (ETOP, Silani et al., 2013) or a monetary game paradigm (EMOP, Steinbeis et al., 2014) to induce EEB, the use of taste allowed first time to elicit strong enough positive and negative emotions and thus a robust EEB in children as well as adults with the same paradigm. As hypothesized, children between the ages of 7 to 12 showed a significantly larger EEB compared to adults, which was double in size of adults' and decreased with age. Importantly, only conflict processing and none of the other cognitive and affective abilities showed a robust association with individual differences in the EEB. Indeed conflict processing was the only one of the many cognitive and affective functions assessed that mediated the developmental differences observed in EEB between children and adults. This finding suggests that children's difficulty in overcoming emotional egocentricity seem to be best explained by their difficulties in conflict processing. Additionally it was found that emotional egocentricity and cognitive egocentricity in children were unrelated to each other importantly suggesting that developmental

egocentricity might partly represent a domain-specific phenomenon. Chapter 2 will present the study outlined above.

1.7.2 Study 2

Study 2 aimed to investigate first behaviourally whether individuals with ASD compared to matched healthy controls would show normal emotional egocentricity as measured through the EEB Touch-Paradigm (ETOP, Silani et al., 2013), but exhibit known ToM deficits. The second part of study 2 aimed to shed light on the neuronal networks underlying a potential dissociation between overcoming cognitive and emotional egocentricity in ASD and their respective dysfunction based on a resting-state functional connectivity analysis seeding from rTPJ and rSMG respectively in an independent large multi-center sample of individuals with ASD and matched healthy controls.

The results of part 1 of study 2 showed that individuals with ASD, while displaying impairments in ToM, exhibited normal emotional egocentricity comparable in size to healthy controls. This finding suggests that individuals with ASD have relatively spared self-other distinction during empathic relating. Additionally, only ToM abilities were related to symptom severity in ASD, while emotional egocentricity as measured by the ETOP, was totally unrelated. The results of part 2 of study 2 nicely complimented the behavioural findings of part 1. The rSMG, relative to rTPJ, was significantly connected to bilateral AI, MCC, i.e., regions which have been consistently shown to play a crucial role in emotion processing such as during interoception and empathy (Lamm et al., 2011; Singer, Critchley, & Preuschoff, 2009; Singer et al., 2004). The rTPJ, relative to the rSMG, was in contrast predominantly connected with PCC, precuneus, MPFC, and ITPJ, all regions commonly associated with cognitive processes such as attentional processing, default mode brain function, as well as mentalizing and cognitive perspective-taking (Buckner, Andrews -

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Hanna, & Schacter, 2008; Carter & Huettel, 2013; Frith & Frith, 2006; Gusnard, Akbudak, Shulman, & Raichle, 2001; Van Overwalle, 2009). These differing resting-state profiles of rSMG and rTPJ are in accordance with similar parcellations of the temporo-parietal junction (Bzdok et al., 2013; Mars et al., 2012). More importantly, the direct comparison of these networks between the healthy control and ASD samples revealed that in line with the behavioural patterns observed in study 1, ASD participants displayed abnormal resting-state connectivity in the ToM network with significantly decreased functional connectivity of the rTPJ to the MPFC, PCC and ITPJ. In contrast, there were no significant functional connectivity differences between individuals with ASD and healthy controls in the rSMG network. Additionally, symptom severity was shown to correlate negatively with increasing rTPJ/PCC coupling, speaking to the importance of the ToM network abnormalities in contributing to autistic symptomatology.

In sum, study 2 demonstrated that individuals with ASD show normal emotional egocentricity i.e. intact self-other distinction during empathy, which links to an unimpaired rSMG network. In contrast ToM abilities in ASD were shown to be deficient and mirrored in aberrant resting-state connectivity within the rTPJ network. These findings add to a further refined characterization of social deficits in ASD, providing novel evidence for spared crucial socio-affective abilities. The study summarized here will form Chapter 3 of this dissertation.

1.7.3 Study 3

Study 3 aimed to investigate empathic relating in depression more fully, in further elucidating the role of alexithymia, while also looking at empathic relating under simple and complex conditions. To do so healthy controls and depressed patients with low and high alexithymia performed the ETOP, which allows to vary the congruency of emotional perspectives of self and other, thus enables to investigate empathic simulation, as well as self-other distinction during empathy. The results showed that as expected alexithymia but not depression

decreased empathic relating under the simple condition, suggesting empathic simulation is intact in depression when no alexithymia is present. In contrast depressed patients showed deficits in empathic relating under the complex condition independently of alexithymia, when emotional perspectives of self and other differed. Depressed patients exhibited increased egocentric bias during empathic judgments compared to healthy controls under the complex condition, suggesting a difficulty in detaching from their own emotional perspective to empathically judge the incongruent emotional perspective of another person. Additionally depressed patients also showed an increased altercentric bias during emotional self judgments compared to healthy controls that was independent of alexithymia. This suggests that a heightened emotional contagion in depression towards other people's emotional perspectives. Indeed the degree of emotional contagion as measured by the altercentric bias was positively associated with the average length of the episode, seemingly playing a crucial role in perpetuating the depressive state. Lastly alexithymia affected only the egocentric bias during empathic judgment, in decreasing its size, while emotional contagion was not affected by alexithymia.

In sum the findings of study 3 suggest that depressed patients show intact empathic judgments, when simulation is not hampered by concurrent alexithymia. Under more complex conditions however, when emotional perspectives of self and other differ, depressed patients show increased egocentric bias during empathic judgments and heightened emotional contagion. The whole study is presented in detail in Chapter 4.

1.8 Considerations, limitations and perspectives

The studies presented in this dissertation further advance the knowledge in their respective fields. While previous research has investigated the neural correlates of emotional egocentricity in adults and children, the underlying mechanism of developmental emotional egocentricity had not been identified. Study 1 delivered evidence for conflict processing as an underlying mechanism mediating age-related differences in emotional egocentricity. Additionally studies 2 and 3 were the first to investigate emotional egocentricity in two mental disorders, namely autism and depression which both have been commonly characterized by broad social cognitive deficits. The findings of study 2 showed that self-other distinction during empathic relating as indicated by normal emotional egocentricity, remains spared in ASD, based on intact functioning of the rSMG network. This adds to previous findings that some important socio-affective abilities are indeed spared in ASD. Study 3 showed that MDD patients do show increased egocentric bias during empathic relating, independently of alexithymia. Alexithymia and not depression decreased simple empathy, but did also decrease the egocentric bias when emotional perspectives of self and other differed. Additionally MDD patients displayed an increased altercentric bias during emotional self judgments, which represents a form of heightened emotional contagion. These findings describe the nature of empathy deficits in depression more fully in suggesting that empathic relating is intact in MDD patients, as long as emotional states of self and other are congruent and no alexithymia is present, but deficient if emotional states of self and other differ and empathic relating becomes more complex. Further research is needed to elucidate the underlying mechanisms of these specific deficiencies in empathic relating in depression.

In the next sections methodical and theoretical considerations that directly follow from these 3 studies will be discussed. Afterwards implications for intervention and society will be proposed.

1.8.1 Methodical Considerations

The role of conflict processing in relation to developmental emotional egocentricity in children needs to be further investigated. As in study 1 just an emotional and not also an additional non-emotional Flanker task was used to measure conflict processing, the role of solving an emotional conflict in contrast to a non-emotional conflict in relation to emotional egocentricity remains to be clarified. fMRI findings have reported different neural correlates for emotional and non-emotional conflict processing (Egner et al., 2008; Etkin, Egner, Peraza, Kandel, & Hirsch, 2006), possibly suggesting that the role of solving a specifically emotional conflict to overcome emotional egocentricity might be of importance. Future studies are needed to address this issue.

As developmental emotional egocentricity has been related to conflict processing abilities, it would be viable to assume that conflict processing also plays a role in psychopathological emotional egocentricity during empathic relating of MDD patients. In this case the same underlying mechanism could explain developmental and psychopathological emotional egocentricity. The previous finding of the decreased coupling of DLPFC and rSMG in children during overcoming emotional egocentricity (Steinbeis et al., 2014), could refer to the deficient ability in resolving the emotional conflict of the emotional perspectives of self and other. DLPFC functioning has been associated with conflict processing and particularly the resolution of conflict (Badre & Wagner, 2004; Egner et al., 2008), while both has been found to be deficient in depression (Grimm et al., 2008; Wolkenstein, Zeiller, Kanske, & Plewnia, 2014). Future studies should investigate the role of conflict processing in increased egocentric bias during empathic judgments in depression. For future investigations it would be of interest to use different attention modulations within the emotional egocentricity paradigms to decrease and increase emotional egocentricity. By increasing the saliency of the emotional state of the other, the emotional conflict between self and other should be easier to overcome, leading to decreased emotional egocentricity.

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It could be argued that the emotional egocentricity paradigms used do not require meta-representations, whereas typical false belief tasks do. The emotional egocentricity paradigms are closer to level 1 visual perspective taking tasks, where mental states of both self and other might differ, but refer to different objects of reference, thus not necessarily needing a conceptualisation of different mental perspectives about the world (Moll & Tomasello, 2006). Like level 1 visual perspective taking in which participants are asked ‘what they see’, EEB paradigms ask participants ‘what they feel’. It would be interesting therefore to let participants make differing emotion judgments on the same object or event of reference, asking the question of “how they feel”. This could be for example established in using the same symbol, meaning a negative stimuli for one participant and a positive stimuli for the other participant. Such an experimental investigation seems of relevance as people often have contrary views, beliefs and emotional reactions towards the same object or event in the world. For example some people might like the taste of peas, whereas others might totally dislike it. Indeed some interesting questions would arise from such a “level 2 emotional egocentricity paradigm”. First of all behaviourally it would be interesting whether emotional egocentricity as measured with such a “level 2 emotional egocentricity paradigm” would be related to emotional egocentricity measured with the established old paradigms (“level 1 emotional egocentricity paradigm”). Concerning underlying mechanisms, it could be assumed that response inhibition rather than conflict processing might be more related to overcoming such an emotional egocentricity, as the particular emotional meaning of the object or event for oneself has to be inhibited to really take into account the contrary emotional perspective of another person. Importantly as a “level 2 emotional egocentricity paradigm” would make more demands on working memory than a “level 1 emotional egocentricity paradigm”, one would have to control for this. On the level of the brain it would be interesting whether in such a “level 2 emotional egocentricity paradigm” also the rSMG would be recruited or

whether the use of possibly meta-representational capacities in the emotional domain would recruit rTPJ instead or in addition, as is the case for false belief reasoning.

1.8.2 Theoretical considerations

Following from the methodological discussion the question of the ecological validity of these studies arises. While placing participants in a relevant social context, which already establishes a greater ecological validity than in many other social cognition studies, the used experimental setups resemble by no means any kind of real life social interaction. The lack of ecological validity does however not diminish the applicability of the findings presented. However further support of the emotional egocentricity phenomenon and its real-life relevance would be achieved by the elucidation of relations to other relevant social behaviours, such as prosocial behaviours.

An important consideration that arises particularly in developmental studies but also in psychological studies in general is the debate of motivation versus competence (Benabou & Tirole, 2003; Chevallier, Kohls, Troiani, Brodtkin, & Schultz, 2012; Kanfer & Ackerman, 1989; Malti, Gummerum, Keller, & Buchmann, 2009; Wigfield & Guthrie, 1997). It has been proven difficult to disentangle the two, as most experimental designs do not assess motivation in participants. Similarly the used emotional egocentricity designs in our studies do not account for motivation. Deficits in executive functions in children for example, such as conflict processing, have commonly been interpreted as deficits in competence, which have knock-on effects on other cognitions, such as social cognitions. For example the success children display on solving implicit ToM tasks before the age of 4 suggest that problems in passing explicit ToM tasks, might have to do with competence rather than motivation (Senju, 2012; Senju et al., 2010). Also children's difficulty in visual perspective taking has been suggested to relate to making an explicit choice and resolve the conflicting perspectives of self and other (Epley, Morewedge, & Keysar, 2004). Similarly the association of conflict

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processing and increased emotional egocentricity in children in study 1 might point to a problem of competence, rather than motivation. Despite these hints, the influence of motivation in overcoming emotional egocentricity cannot be ruled out. Similar reasoning would apply when interpreting emotional egocentricity in depression. The presence of an altercentric bias during emotional self judgments in depression suggests intact spontaneous empathic relating in these patients, and instead an inability to detach emotional perspectives of other's from one's own emotional perspective. Thus, it could be argued that the mechanism of solving conflicting perspectives is deficient in depression, which might be less influenced by motivational differences, in comparison to mechanisms of empathic relating. However this remains purely speculative and only studies that have means of measuring motivation can surely talk about its influence and role.

1.8.3 Implications for intervention

Identifying underlying mechanisms of developmental and psychopathological emotional egocentricity can have wide ranging implications for intervention at the level of the individual. Abnormal egocentricity can have detrimental effects for an individual in integrating into its social environment particularly as there are high interpersonal costs involved in not fully comprehending another's point of view (Newcomb, Bukowski, & Pattee, 1993; Thompson & Loewenstein, 1992). This becomes of huge importance for a developing child which has to negotiate its place as social self within its environment. Psychopathological emotional egocentricity such as in depression prevents individuals from reintegrating into his/her social environment, while particularly representing an obstacle for therapeutic success, which is largely mediated through a therapeutic alliance build on empathy and trust (Burns & Nolen-Hoeksema, 1992; Lambert & Barley, 2001). With identifying conflict processing as an underlying mechanism of increased emotional egocentricity in children, potential interventions can be envisioned to tackle abnormal emotional egocentricity early in

development. Conflict processing training could help to reduce the conflict experienced by children when emotional perspectives of self and other differ, leading to a more accurate empathic judgment. As empathy has been linked to pro-sociality (Batson & Shaw, 1991; Eisenberg, 2000; Eisenberg et al., 1989; Hein, Lamm, Brodbeck, & Singer, 2011; Hein, Silani, Preuschoff, Batson, & Singer, 2010) this would potentially have beneficial effects on the prosocial and moral development of children. In a similar manner, once the underlying mechanisms of emotional egocentricity in depression are identified, appropriate targeted interventions could be designed. Mindfulness-based therapy which already has been shown to reduce depressive symptoms (Hofmann, Sawyer, Witt, & Oh, 2010; Paul, Stanton, Greeson, Smoski, & Wang, 2013), might be also be very useful in reducing abnormal emotional egocentricity in children and depressed patients, as it trains executive functions (such as conflict processing) as well as interoception (Farb, Segal, & Anderson, 2012; Hölzel et al., 2011; Hölzel et al., 2007), which both play a functional role in emotional egocentricity. It should be noted that other therapeutic approaches will possibly rely on similar modes of action and will most likely be effective for decreasing emotional egocentricity.

1.8.4 Societal relevance

There have been signs in society that egocentrism is on the rise. Some scholars have for example reported that narcissism as an extreme manifestation of egocentrism seems to increase among the members of society (Paris, 2014; Twenge, Miller, & Campbell, 2014). This unfavorable development could be seen as consequence of a modern society being characterized by an “expressive individualism” (Bellah, Madsen, Sullivan, Swidler, & Tipton, 1985), violently endorsing the freedom of the individual, and its need for self-fulfillment. While more evidence is needed some already speak of a ‘narcissism epidemic’ (Paris, 2014; Twenge et al., 2014). It seems thus that if at some point in an individualistic society the only thing which can be agreed upon is the freedom of the individual, this society will devour

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itself. Then egocentricity could indeed become an epidemic in society spreading among its members, gnawing at its very foundation, which should be the integral pillars of mutual understanding, trust, the means of shared values and the pursuit of shared goals. Investigating the causes of emotional and cognitive egocentricity in adults but also in child development and psychopathology seems an important scientific endeavour, which could play its part in helping to prevent this “egocentric epidemic” from spreading. It comes to no surprise that nowadays society could be threatened by divide more than ever. In these fast moving times, and a world growing ever more global, humanity seems to shrink to a mass of selves. Globalization will pose increasingly more demands for the world community, which will not be met, if egocentricity cannot be overcome.

2. Manuscript of Study 1

**Children's increased emotional egocentricity compared to adults is
mediated by age-related differences in conflict processing**

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Abstract

This study investigated the cognitive mechanisms underlying age-related differences in emotional egocentricity bias (EEB) between children (aged 7-12 years, $N = 30$) and adults (aged 20-30 years, $N = 30$) using a novel paradigm of visuo-gustatory stimulation to induce pleasant and unpleasant emotions. Both children and adults showed an EEB, but that of children was larger. The EEB did not correlate with other measures of egocentricity. Crucially, the developmental differences in EEB were mediated by age-related changes in conflict processing and not visual perspective taking, response inhibition, or processing speed. This indicates that different types of egocentricity develop independently of one another and that the increased ability to overcome EEB can be explained by age-related improvements in conflict processing.

Introduction

Human interpersonal understanding often relies on mechanisms of self projection and simulation (e.g. Mitchell, 2009; Nickerson, 2001; Silani et al., 2013; Van Boven & Loewenstein, 2003). These mechanisms however become inefficient as soon one's own mental state or internal experience differs to that of another person. For instance it would be erroneous to assume someone was happy while he clearly is sad just because we ourselves feel happy. The tendency to project one's own mental states onto others has been broadly termed as egocentricity bias. Early and seminal work in developmental psychology has looked at children's ability in taking visual perspectives of another person, reporting early egocentrism in development, one example being Piaget's famous 'three mountains' task, in which children at the age of 7 exhibit difficulties judging someone else's visual perspective which differs from their own (Piaget & Inhelder, 1956). To date egocentricity bias has thus been primarily investigated in visual perspective taking and Theory of Mind (Birch & Bloom, 2007; Flavell et al., 1981; Pronin, 2008; Royzman et al., 2003; Thomas & Jacoby, 2012). Children generally exhibit stronger egocentricity during cognitive perspective taking and Theory of Mind tasks than adults. Before the age of 4 children have difficulties attributing false beliefs to other people, unable to detach from their own true beliefs (Wimmer & Perner, 1983). Also, throughout childhood difficulties in cognitive perspective taking and Theory of Mind (ToM) seem to persist (Apperly et al., 2011; Keysar et al., 2003; Sommerville et al., 2013). While strong evidence for egocentricity in the cognitive domain in children as well as adults has accumulated over the past decades, very little research focused on investigating egocentricity in the affective domain (see O'Brien & Ellsworth, 2012; Repacholi & Gopnik, 1997; Silani et al., 2013; Van Boven & Loewenstein, 2003) and only one study has so far looked specifically at emotional egocentricity in children (Steinbeis et al., 2014).

Egocentricity is a pervasive phenomenon throughout childhood, spanning moral judgments (e.g. Eisenberg et al., 1987), taking the visual perspective of others (e.g. Moll &

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Tomasello, 2006), and assuming others' mental states (e.g. Sommerville et al., 2013). However, whether egocentricity constitutes a unitary phenomenon in development and whether age-related changes in the extent of egocentricity undergo shared developmental trajectories remains unclear. Data from meta-analyses and neuroimaging findings in adults suggest in part that cognitive egocentricity and emotional egocentricity are dissociable at the neural level (Silani et al., 2013). Using visuo-tactile stimulation to induce pleasant and unpleasant emotional states in participants (EEB Touch-Paradigm, ETOP), Silani et al. (2013) demonstrated that right supramarginal (rSMG) is functionally implicated in overcoming EEB. Peaks of this activation were shown to be distinct from other subregions of temporo-parietal cortex involved in Theory of Mind and motor egocentricity. However, seeing that cognitive capacities and abilities are known to increasingly differentiate with development (e.g. Li et al., 2004) it is unclear if these various types of egocentricity correlate in development or not. Shedding light on this question is crucial, given the high interpersonal costs associated with not fully comprehending another's point of view (Newcomb et al., 1993; Thompson & Loewenstein, 1992). Understanding the mechanisms that underlie the inability to overcome such egocentricity early in ontogeny seems an important endeavor as it can provide the basis for targeted interventions leading to greater pro-sociality early in development.

First attempts to uncover the developmental mechanisms that help to overcome EEB were recently made in a study (Steinbeis et al., 2014) using monetary reward and punishment to induce pleasant and unpleasant emotions in children and adults (EEB Monetary Game Paradigm, EMOP). Children (aged 6 to 13) showed a significant EEB, which was significantly larger compared to adults. In line with the study by Silani et al. 2013, on the neuronal level children showed significantly less activation of rSMG compared to adults when having to overcome EEB, as well as reduced coupling between rSMG and left dorsolateral prefrontal cortex (DLPFC). In addition children and adults also performed a belief and desire reasoning task, an attentional reorientation task and a Stop-signal reaction

time task (SSRT). None of these variables showed a relationship with the EEB in children or adults. Thus, while prior work has shown that the EEB is larger in children compared to adults and provides a coherent account of the neural mechanisms leading to this developmental change, what is still missing and has not been addressed in previous studies, is a systematic analysis of the exact cognitive and affective mechanisms that may account for observed age-related differences in the size of EEB during development.

In order to address this question we developed a novel paradigm, the EEB Taste-Paradigm (ETAP) using visuo-gustatory stimulation in which participants are asked to judge the pleasantness of their own taste experiences or that of another person, while both can have congruent or incongruent taste experiences. Pilot work indicated that gustatory stimulation elicits equal feelings of pleasantness and unpleasantness in children and adults, making it highly suited to study developmental differences in EEB as well as extending the phenomenon of EEB to another stimulus modality. As in the previous study (Steinbeis et al., 2014), we expected that children would show an increased EEB compared to adults. Overcoming such EEB presumably relies on a multitude of higher- and lower-level cognitive and affective processes. With the aim to comprehensively test for these possible processes underlying the developmental differences in EEB we assessed them using a large battery of tasks. In the following a more detailed description of reasons for investigating particular cognitive and affective processes in relation to EEB and developmental differences in EEB are given.

The EEB paradigm involves taking an emotional perspective of the other. In that process the role of rSMG seems crucial in overcoming affective egocentricity, which has been interpreted as disambiguating emotional self and other perspectives (Silani et al., 2013; Steinbeis et al., 2014). As argued previously, it might therefore relate to other types of egocentricity. To explore this, we investigated visual perspective taking with a task more

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closely matched to the EEB paradigm involving incongruent and congruent self and other visual perspectives to measure cognitive egocentricity (see Surtees & Apperly, 2012).

The EEB paradigm also involves the inhibition of one's own conflicting emotional perspective to correctly judge the other person's emotional state. From the literature in the domain of cognitive perspective taking, such as Theory of Mind it is known that inhibitory control plays a crucial role, in particular when there is a conflict between self and other perspectives (Carlson & Moses, 2001; Friedman & Leslie, 2005; Hansen Lagattuta, Sayfan, & Harvey, 2013; Wellman, Cross, & Watson, 2001). Consequently we included a Go/NoGo task measuring response inhibition, moreover, as it is also known that inhibitory control improves throughout development (e.g. Luna, Garver, Urban, Lazar, & Sweeney, 2004; Williams, Ponesse, Schachar, Logan, & Tannock, 1999).

Another executive function which could potentially be an underlying mechanism of EEB and the developmental difference in EEB is conflict processing. The ability to resolve a conflict has been hypothesized to be a crucial process to overcome the EEB when emotional states of self and other are incongruent. It is also known that the ability to resolve conflict improves across development (e.g. Fjell et al., 2012), and could therefore account for developmental differences in EEB.

Another high-level cognitive-affective process of interest for this study was cognitive reappraisal as a form of emotion regulation (Gross, 2002). The ability to cognitively reappraise one's own emotion and subsequently down-regulate the emotion might be crucial in overcoming EEB. Findings additionally suggest that children tend to be less efficient in cognitive reappraisal than adults (McRae et al., 2012; Pitskel, Bolling, Kaiser, et al., 2011).

One key process that the EEB might be explained by is attentional reorienting, something which has been consistently associated with the involvement of rSMG (Carter & Huettel, 2013; Mars et al., 2012). So far, no association has been found between measures of attentional reorienting and the EEB neither at the neural level nor at the behavioural level

(Silani et al., 2013; Steinbeis et al., 2014) and age-related changes in attentional reorienting could not account for the observed developmental differences in the EEB (Steinbeis et al., 2014). Given the differences between the paradigms used to induce the EEB, (primary sensory information vs. abstract monetary rewards and punishments in Steinbeis et al., 2014), we still included an attentional reorienting task, also with the aim to further the evidence of the EEBs independence of attentional reorienting.

Finally, we also investigated general perceptual speed and its relation to overcoming emotional egocentricity in children and adults. Perceptual speed can be seen as a very low level-process that could underlie the EEB and its developmental difference between children and adults, especially as it has been known that it improves continuously throughout development (Kail, 1991; Luna et al., 2004).

In sum, we comprehensively tested various different cognitive, attentional, socio-affective abilities, namely visual perspective taking, response inhibition, conflict processing, emotion regulation, attentional reorienting and processing speed, with the aim of systematically elucidating the exact affective and cognitive mechanisms that underlie age-related differences observed in the EEB between children and adults.

Methods

Children and adults were invited for three experimental sessions. The first session involved a screening, in which the most pleasant, unpleasant and neutral liquids for each participant were selected. In the second session children and adults performed the EEB Taste-Paradigm (ETAP). In the last session children and adults performed a battery of tests assessing different cognitive and affective abilities. The order of the tasks in the last session was counterbalanced across subjects.

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Participants

Thirty children (15 female; mean age = 9.50; range = 7–12) and adults (15 female; mean age = 24.10; range = 20–30) took part in the study. Children and adults were recruited from databases at the Max Planck Institute for Human Cognitive and Brain Sciences. Participants were predominantly White Caucasian. All children were normal developing. All participants gave informed consent (parental consent in case of the children) and the study was approved by the ethics committees of the University of Leipzig (Nr. 381-11-12122011). One child and one adult could not be invited for the third session.

First Session

Screening. In a screening participants were asked to rate different liquids and solutions according to their intensity and pleasantness. Participants were screened for their taste sensitivity using a labeled magnitude scale (LMS) (Green et al., 1996), in order to exclude possible “super/non-tasters” (e.g. Small et al., 2003). On the LMS scale perceived taste intensity ranged from 0 (barely detectable) to 100 (strongest imaginable). Only participants in the normal range of tasting for Glucose and quinine/ NaCl solution (1Mol) participated in the study. The normal taste range for Glucose was defined as lying between 15 and 75, for quinine and NaCL solutions between 30 and 75 (see also Jabbi, Swart, & Keyzers, 2007). For each participant the two most pleasant, the two most unpleasant, and the two most neutral stimuli were selected and used for the later experiment to guarantee the most effective induction of emotions in participants. As pleasant tastes a sugar solution (1 Mol Glucose) and three different juices (apple/Samanta, orange/Samanta, grape/albi) were used. For unpleasant tastes, three salty solutions (NaCL) of varying concentrations of 0.1, 0.5 and 1 Mol (see e.g. O'doherty, Rolls, Francis, Bowtell, & McGlone, 2001) and a quinine solution (0.25mM) were used. For neutral tastes, tasteless solutions with the main ionic components of saliva

(consisting of 25 mM KCl and 2.5 mM NaHCO₃) were used, diluted with various amounts of water (20%, 40%, 60%, 80%).

Second Session

Stimuli and apparatus. For the experimental session the different tastes were presented with a custom-built pump-system specifically designed for this study via several small plastic tubes (diameter = 0.3 cm), which merged together at the end into a mouthpiece with small bundled tubes (diameter = 0.1 cm). The mouthpiece was comfortably placed in the mouth of the participants with the help of a holder to which the tubes were attached so that both hands of the participants were free and able to navigate the touch screen (1920 x 1080 pixels resolution, 19 inch screen, viewing distance ~ 40 cm). The pump system was operated by a Presentation script via a USB connection and was set-up to always pump the same amount of liquid in the same time through the tubes (0.5 ml/0.5s).

EEB Taste-Paradigm (ETAP). The design and procedure of this study was similar to a previous study using the EEB Touch Paradigm (ETOP, Silani et al., 2013). Participants of the same gender, unknown to each other were assigned pairwise to an experimental session. They sat back to back in front of a touch screen unable to see the other person's face and emotion judgments, with the taste tubes comfortably placed in their mouth. This meant that any influence of the other participant's actual emotional state could not have any influence on ratings, as the emotion judgment was exclusively made through the visual cue of what the other was currently experiencing. Before the start of the experiment participants were familiarized with the rating scale and performed 10 practice trials for each condition. Participants started with the individual conditions in which they were instructed to either judge the pleasantness of their own taste experience or judge the pleasantness of the taste experience for the other person (blocked design). In the individual self condition, 500 ms before the taste stimulation a picture (size 500 x 400 pixels) corresponding to the specific taste (i.e. a picture of a glass of orange juice when the participant received orange juice)

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appeared on the screen and remained there until the end of the taste stimulation which lasted 1500 ms. Immediately after the end of the tasting phase participants had to judge the experienced pleasantness or unpleasantness of the taste by using a rating scale (ranging from -10 to +10) on the touch screen, within 1500 ms response time. After the emotion judgment a picture with a water drop appeared on the screen and water was pumped simultaneously through a tube for a rinse. The rinse lasted for 2000 ms followed by an instruction to swallow (1000 ms) and a fixation cross (2000 ms). In the individual other condition, the trial structure remained the same, but with the important difference that the participant did not receive any taste stimuli and was instead instructed to judge the pleasantness or unpleasantness of the taste experience for the other participant also present in the room based on the picture which indicated what taste the other person received. Each run for adults consisted of 30 pseudo-randomized trials, with 10 pleasant, 10 neutral and 10 unpleasant visuo-gustatory stimuli. Each run for children consisted of 18 pseudo-randomized trials, with 6 pleasant, 6 neutral and 6 unpleasant visuo-gustatory stimuli. For the individual conditions this resulted in a three-factorial mixed design with the two within-group factors *target* (self, other judgment) and *valence* (pleasant, neutral and unpleasant stimulation) and the between-group factor *age group* (children and adults).

The individual conditions were followed by the simultaneous conditions. In these simultaneous conditions both participants in the room received taste stimuli simultaneously, and were instructed to either judge the pleasantness of their own taste experience (simultaneous self condition) or judge the pleasantness of the taste experience for the other person (simultaneous other condition). The simultaneous self and simultaneous other conditions were blocked and counterbalanced. In these conditions two pictures appeared on the screen. The left picture was labelled “Self” on the top and corresponded to the taste the participant received, while the right picture labelled “Other” corresponded to the taste the other person received. The taste experiences of the two participants could be either affectively

congruent (e.g. both receive positive tastes) or incongruent (e.g. one receives positive, the other negative taste). The EEB was defined as the difference between ratings in incongruent and congruent trials when judging the other, as compared to the difference when judging one's own feelings. Importantly for the simultaneous conditions the self judgment therefore was used as a control for general perceptual or cognitive confounds- such as visual and affective stimulus comparison, detection of incongruency, or overcoming general response conflict. In the simultaneous conditions for adults each run consisted of 40 pseudo-randomized trials, with 20 pleasant (10 congruent and 10 incongruent) and 20 unpleasant (10 congruent and 10 incongruent) visuo-gustatory stimuli. For the simultaneous conditions for children each run consisted of 24 pseudo-randomized trials, with 12 pleasant (6 congruent and 6 incongruent) and 12 unpleasant (6 congruent and 6 incongruent) visuo-gustatory stimuli. Simultaneous conditions were blocked according to target, so that half the participants started with the self judgment and half of the participants started with the other judgment.

This resulted in a four-factorial mixed design with the three within-group factors *target* (self, other judgment), *valence* (pleasant, unpleasant stimulation), and *congruence* (congruent, incongruent stimulation of participant and other) and the between-group factor *age group* (children and adults). Data analysis was performed using the IBM SPSS statistics software, version 19.0.

Third Session

Visual perspective taking. To assess children's and adults' visual perspective taking abilities we used an established paradigm shown to work well for both children and adults (for details see Surtees & Apperly, 2012). In this paradigm participants heard instructions while they viewed a cartoon avatar standing in a cartoon room with dots on the wall. The auditory stimulus asked them to judge how many dots they perceive (self condition) or how

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many dots the avatar perceives (other condition). The participants then had to respond with the appropriate key with “Yes” or “No” (see Surtees & Apperly, 2012). Self trials as well as other trials could be either consistent or inconsistent depending on whether both participant and avatar saw the same number of dots or not. A possible “egocentric” interference would be described as an increase in response time and error rate for participants judgements on inconsistent other trials compared to consistent other trials (Surtees & Apperly, 2012). One adult participant had to be excluded from analysis, as he clearly misunderstood the task.

Inhibitory control. Inhibitory control in children and adults was assessed with two different Go/NoGo tasks. An emotional Go/NoGo task which used happy and a fearful face stimuli as Go and NoGo stimuli (for details see Hare et al., 2008), as well as a normal Go/NoGo task (same design) using a blue square as a Go stimuli and a red square as a NoGo stimuli (intertrial intervals; 1000 ms, 1500 ms, 2000 ms, 2500 ms, 3000 ms). In these tasks participants had to respond quickly with a button-press to the presentation of Go stimuli, while withholding a response to the presentation of NoGo stimuli. Response inhibition was measured by the ability to inhibit the response to NoGo stimuli. D-primes scores for both Go/NoGo tasks were calculated as a measure of response sensitivity ($d' = Z(\text{hit rate}) - Z(\text{false alarm rate})$).

Conflict processing. To assess conflict processing participants performed a Flanker task using emotional faces (e.g. Fenske & Eastwood, 2003). Participants had to respond as quickly as possible with their right index and middle fingers using the arrow buttons on the keyboard to happy and angry target faces (NimStim faces, Tottenham et al., 2009), which were presented in the centre of the screen (picture size: 101 X 130 pixels). These target faces were flanked by eight distractor faces (picture size: 101 X 130 pixels) which were either all identical or opposite in their emotion displayed relative to the target face. The distractor faces appeared directly around the target faces in angles of 0°, 45°, 90°, 135°, 180°, 225°, 270°,

315°, building in total a 3 x 3 grid with the target faces perfectly adjacent directly in the centre of the grid. A trial was considered to be compatible if the target face was flanked by identical faces portraying the same emotion and considered incompatible if the target was flanked by affectively opposite but same identity faces. The eight distractor faces preceded the target face (100 ms, 200 ms, or 300 ms), and remained on the screen together with the target until a response was given (1000 ms). Trials were always followed by a random intertrial interval (500 ms 1000 ms, 1500 ms). In total there were 96 trials, 48 compatible trials and 48 incompatible trials (24 happy and 24 angry targets). The trial order was randomized for each participant. All participants were instructed to respond as quickly as possible. An increase in response time (on correct trials) and error rates in incompatible compared to compatible trials indicates a so called flanker compatibility effect (Eriksen & Eriksen, 1974).

Emotion regulation. We specifically developed a new task in which participants were instructed to regulate their own taste experiences. To most closely match the demands of the emotion regulation task to the demands of the ETAP, the same tastes and the same taste pictures were used, as well as the same length of taste stimulation. Participants were instructed to either taste the liquids normally or to reappraise their taste experience as weaker and less strong (taste or regulate), which was indicated by a picture cue remaining on the screen for 4000 ms (see e.g. Pitskel, Bolling, Kaiser, Crowley, & Pelphrey, 2011). This was followed by a gustatory stimulation of 1500 ms. Afterwards participants judged the pleasantness or unpleasantness of the taste by tapping on a rating scale (ranging from -10 to 10) on the touch screen, within 4000 ms response time. Afterwards an instruction to relax appeared on the screen for 3000 ms, followed by an intertrial interval of 2000 ms. The experiment consisted of 10 reappraising trials (5 positive, 5 negative), and 20 normal taste trials (5 positive, 5 negative, 10 neutral) in a pseudorandom order. If participants seemed to

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use other strategies (distraction, suppression) during the training, they were informed about it and instructed to use reappraising strategies instead.

Attentional reorienting. Attentional reorienting was assessed using the “attentional cueing” paradigm (for details see Mitchell, 2008). In this task participants were instructed to indicate by pressing the left or right arrow key on the keyboard, the location of a visual target stimulus on the left or the right side of the computer screen. The location of the visual target was either congruent or incongruent to a preceding arrow pointing to the left or to the right. Typically response times and error rates have been shown to be increased in the incongruent condition compared to the congruent condition (Mitchell, 2008). Because of a technical problem data from one adult could not be obtained.

Processing speed. To assess processing speed, children and adults performed a reaction time task (for details see Deary, Der, & Ford, 2001). For simple reaction time a grey square appeared on the screen and participants had to press the corresponding button (grey button) with their index finger. For the four-choice reaction time participants rested the second and third finger of each hand on the colored keys (pink, brown, red, blue) and pressed the corresponding button when a colored square appeared on the screen. Because of technical problems data of 5 children could not be obtained.

Results

EEB Taste-Paradigm (ETAP)

Individual conditions.

Ratings. To investigate any group differences in the individual conditions an analysis of variance (ANOVA) on the affective ratings with target and valence as within-subjects factors, and age group as between-subjects factor was performed. Results revealed no

significant main effect of group and no significant interactions of target by group, valence by group or target by valence by group ($F_s < 1.798$, $p_s > .170$). There was a significant main effect of valence, $F(1, 58) = 429,676$, $p < .001$, $\eta_p^2 = 0.881$, but no significant main effect of target, or significant interaction of target by valence ($F_s < 2.836$, $p_s > .098$) indicating that the emotion induction by means of visuo-gustatory stimulation was equally effective for both groups of participants.

Simultaneous conditions.

Ratings. To investigate whether children would display a significantly greater EEB than adults an analysis of variance (ANOVA) on the affective ratings with target, congruency and valence as within-subjects factors and age group as between-subjects factor was performed. The results showed that there was no main effect of age group, $F(1, 58) = 1,442$, $p = .235$, $\eta_p^2 = 0.024$. There were however significant interactions of target and age group, $F(1, 58) = 5,597$, $p < .05$, $\eta_p^2 = 0.088$ and valence and age group, $F(1, 58) = 5,170$, $p < .05$, $\eta_p^2 = 0.082$. Most importantly children showed a significantly larger emotional egocentricity than adults as shown by the triple interaction of target, congruency and age group, $F(1, 58) = 4,553$, $p = .037$, $\eta_p^2 = 0.073$. The EEB was defined as the difference between ratings in incongruent and congruent trials when judging the other, as compared to the difference when judging one's own feelings and calculated accordingly. In fact, the children's EEB was 2.09 times larger than that of the adults (Figure 2.1).

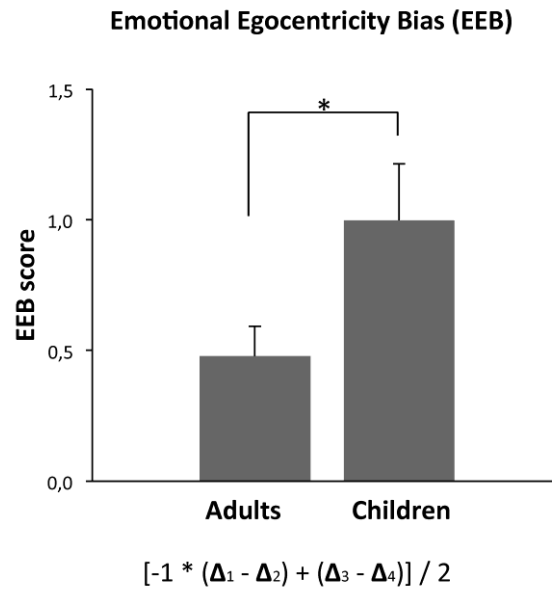


Figure 2.1. EEB (mean + SE) is pooled across pleasant and unpleasant judgments for both children and adults. For descriptive purposes, EEB was explicitly calculated by subtracting other-related emotion judgments (run “other judgment”) during congruent trials from other-related judgments during incongruent trials. From this, as a control, we subtracted the differences between congruent and incongruent trials in the “self judgment” run. Whereas both adults and children show a significant EEB, children’s EEB is significantly larger and more than double the size of the adults.

Further, within the group of children the EEB decreased significantly (one-tailed) with age, $r = -.335$; $p = .035$, meaning the older children were the smaller their emotional egocentricity was.

The results in the children sample revealed main effects of target, $F(1, 29) = 12,727$, $p < .01$, $\eta_p^2 = 0.305$, and congruency, $F(1, 29) = 6,103$, $p < .05$, $\eta_p^2 = 0.174$. There was no main effect of valence, $F(1, 29) = 0,137$, $p = .714$, $\eta_p^2 = 0.005$ (Figure 2.2a).

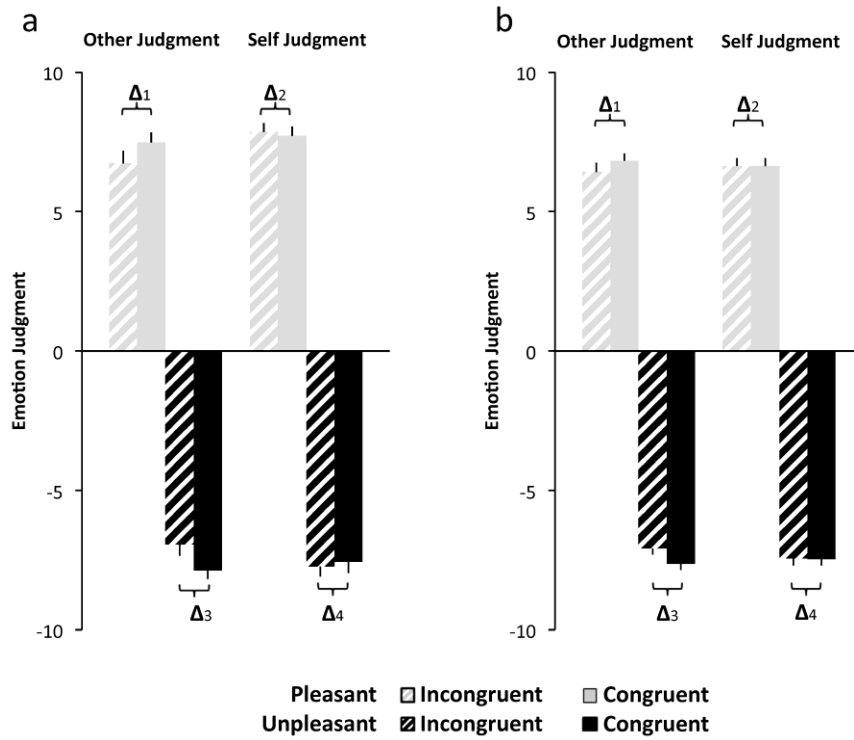


Figure 2.2. (a) Children’s emotion judgments (mean + SE) during the simultaneous conditions are plotted for each condition of the factorial design. (b) Adults’ emotion judgments (mean + SE) during the simultaneous conditions are plotted for each condition of the factorial design.

Children displayed significant emotional egocentricity as indicated by the significant target and congruency interaction, $F(1, 29) = 21,608, p < .0001, \eta_p^2 = 0.427$, showing that the congruency effect was larger when rating the other compared to rating the self. This observed effect in children was 1.2 times larger than in a previous study ($\eta_p^2 = 0.427$ vs. $\eta_p^2 = 0.345$ in Steinbeis et al., 2014). There were no further significant interactions between the variables ($F_s < 2.219, p_s > .147$). The results in the adult sample revealed main effects of valence, $F(1, 29) = 17,646, p < .0001, \eta_p^2 = 0.378$, and congruency, $F(1, 29) = 5,980, p < .05, \eta_p^2 = 0.171$. There was no main effect of target, $F(1, 29) = 0,206, p = .653, \eta_p^2 = 0.007$. Adults displayed significant emotional egocentricity as indicated by a significant target and congruency interaction, $F(1, 29) = 17,346, p < .001, \eta_p^2 = 0.373$ (Figure 2.2b). This observed effect in

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adults was 5.1 times larger than in the in previous study ($\eta_p^2 = 0.373$ vs. $\eta_p^2 = 0.074$ in Silani et al., 2013), which speaks to the suitability of visuo-gustatory stimulation to induce a strong EEB. There were no further interactions between the variables ($F_s < 0.580, p_s > .453$).

We also tested whether differences in processing speed of emotional incongruence between children and adults could influence differences in EEB. For this, we computed an EEB from the response times (RTs) of the simultaneous conditions (computed as the EEB for the ratings) and used it as a covariate. The results however showed that the interaction of target, congruency and age group remained significant, $F(1, 57) = 5,018, p = .029, \eta_p^2 = 0.081$. Similarly, differences in EEB between children and adults could be due to differences in emotion intensity perception. We therefore looked at whether the single self intensity rating (average of positive and negative ratings for self) has any significant influence on the difference in EEB between the two age groups and included it as a covariate. The interaction of target, congruency and age group remained significant, $F(1, 57) = 3,922, p = .026, \eta_p^2 = 0.064$ (one – tailed). These results show that neither differences in processing speed of emotional incongruence nor differences in emotion intensity perception between children and adults can explain the larger EEB in children.

Assessment of cognitive and affective mechanisms

The following describes the results for the tasks performed by children and adults in the third session. First, possible age group differences are reported looking at the interactions with age group, and then main effects of the tasks for children and adults separately. Second, correlations of the different cognitive and affective processes with the EEB are reported first for children and adults separately, and then over the total sample.

Visual perspective taking. To specifically investigate egocentricity in visual perspective taking, analyses were performed on error percentages and responses times for other perspective judgments only.

Error percentages. Looking at age group differences children showed a stronger egocentric interference as indicated by a significant consistency by age group interaction, $F(1, 55) = 4,625, p < .05, \eta_p^2 = 0.078$. These results suggest that children show an increased egocentricity in visual perspective taking compared to adults. For children a significant main effect of consistency emerged, $F(1, 28) = 19,054, p < .001, \eta_p^2 = 0.405$, indicating that children showed significant egocentricity during visual perspective taking. Also for adults a significant main effect of consistency emerged, $F(1, 27) = 15,783, p < .001, \eta_p^2 = 0.369$ indicating that adults showed significant egocentricity during visual perspective taking.

Response times. Looking at age group differences children showed a stronger egocentric interference as indicated by a marginally significant consistency by age group interaction, $F(1, 55) = 3,970, p = .051, \eta_p^2 = 0.067$. For children a significant main effect of consistency emerged, $F(1, 28) = 56,806, p < .001, \eta_p^2 = 0.670$, indicating that children showed significant egocentricity during visual perspective taking. Also for adults a significant main effect of consistency emerged, $F(1, 27) = 71,810, p < .001, \eta_p^2 = 0.727$, indicating that adults showed significant egocentricity during visual perspective taking.

Differences in response times and error percentages between inconsistent other and consistent other conditions were computed as measures of cognitive egocentricity. In both cases larger difference scores indicated greater incongruency costs, therefore greater egocentricity. There was no significant relation between cognitive egocentricity and the EEB for children (RTs: $r = .099, p = .608$; error percentage: $r = -.145, p = .453$) or for adults (RTs: $r = -.055, p = .780$; error percentage: $r = -.106, p = .591$), or for the total sample (RTs: $r = .122, p = .368$; error percentage: $r = -.056, p = .675$).

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Inhibitory control. For the emotional Go/NoGo d-prime score the two different d-prime scores for the emotional target conditions were averaged together as no significant differences were found between response inhibition towards happy and towards fearful targets. Larger d-prime scores indicated greater response sensitivity. To investigate differences in inhibitory control independent samples t-tests were performed on the d-primes measures. Adults showed significantly greater d-prime scores for the emotional Go/NoGo, $t(56) = 6,414, p < .001$, as well as the normal Go/NoGo, $t(56) = 10,255, p < .001$. These results showed that adults exhibited significantly better response inhibition compared to children.

There was no significant relation between response inhibition and the EEB for children. This was the case for the emotional Go/NoGo ($r = -.207, p = .281$) as well as the normal Go/NoGo ($r = -.113, p = .560$). For adults there was also no relation between response inhibition on the emotional Go/NoGo ($r = -.098, p = .612$) and on the normal Go/NoGo ($r = .030, p = .879$) and the EEB. Over the total sample however, there was a significant negative correlation of response inhibition and the EEB on the emotional Go/NoGo ($r = -.269, p = .041$) and a marginally significant negative correlation on the normal Go/NoGo task ($r = -.246, p = .063$), indicating that with decreasing ability in response inhibition the EEB tends to increase.

Conflict processing.

Error percentages. Looking at age group differences there was a significant main effect of age group, $F(1, 56) = 17,339, p < .001, \eta_p^2 = 0.237$. Additionally there was a significant interaction of compatibility by age group, $F(1, 56) = 4,266, p < .05, \eta_p^2 = 0.071$. There were no further interactions with age group and target and age group and target and compatibility ($F_s < 0,091, p_s > .764$). These results indicate that children show a greater compatibility effect than adults pointing towards greater difficulties in conflict processing.

For children there was a significant flanker compatibility effect, $F(1, 28) = 5,081, p < .05, \eta_p^2 = 0.154$, and no significant main effect of target face or target face by compatibility interaction ($F_s < 0,692, p_s > .412$). For adults there was no significant flanker compatibility effect, $F(1, 28) = 0,032, p = .859, \eta_p^2 = 0.001$, and no significant main effect of target face and no significant target face by compatibility interaction ($F_s < 2,449, p_s > .129$).

Response times. Regarding age group differences on response times during correct trials there was a significant main effect of age group, $F(1, 56) = 15,390, p < .001, \eta_p^2 = 0.216$, and a marginally significant interaction of compatibility by age group interaction, $F(1, 56) = 3,860, p = .054, \eta_p^2 = 0.064$. There were no further interactions with group and target, and group and target and compatibility ($F_s < 1,479, p_s > .229$). These results suggest that children did indeed show more difficulties in conflict processing, showing greater compatibility effects in error percentages and also a tendency towards greater compatibility effects in reaction times. For children there was a significant flanker compatibility effect, $F(1, 28) = 26,293, p < .001, \eta_p^2 = 0.484$, a significant main effect of target face, $F(1, 28) = 7,141, p < .05, \eta_p^2 = 0.203$ but no significant target face by compatibility interaction, $F(1, 28) = 1,838, p = .186, \eta_p^2 = 0.062$. Children showed significantly faster responses for happy target faces. For adults there was a significant flanker compatibility effect, $F(1, 28) = 17,634, p < .001, \eta_p^2 = 0.386$, but no main effect of target and no significant target face by compatibility interaction ($F_s < 3,600, p_s > .068$).

A difference in error percentages between incompatible and compatible flanker conditions was computed as a measure of conflict processing. A larger difference score indicated greater compatibility effects, therefore less efficient conflict processing. There was a significant relation between conflict processing and the EEB for children ($r = .387, p < .05$) but not for adults ($r = .031, p = .871$). Further, there was a significant positive relation between conflict processing and the EEB over the total sample ($r = .373, p < .005$). This

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significant association between conflict processing and the EEB remained even after controlling for response inhibition as measured by the Go/NoGo tasks.

Emotion regulation. Looking at age group differences there was no significant condition by age group interaction, $F(1, 56) = 0,606, p = .404, \eta_p^2 = 0.011$, and no further significant effects with age group ($F_s > 0,398, p_s > .531$). These results suggest that children and adults reappraised their taste experiences equally well in this novel emotion regulation task. There was a significant effect of condition for children, $F(1, 28) = 57,202, p < .01, \eta_p^2 = 0.671$ as well as for adults, $F(1, 28) = 98,454, p < .01, \eta_p^2 = 0.779$. There was no significant main effect of emotion ($F_s < 1,614, p_s > .210$) and no significant interaction of emotion by condition for children and adults ($F_s < 1,047, p_s > .315$). These results indicate that children and adults were successful at reappraising their taste experiences and were so equally well for negative and positive tastes.

A reappraisal score was computed as a measure of emotion regulation success (difference between ratings in the taste condition and the regulate condition). Larger scores indicated higher reappraisal ability. There was no significant relation between reappraisal ability and the EEB for children ($r = -.123, p = .529$) or for adults ($r = .166, p = .389$) or for the total sample ($r = -.023, p = .867$).

Attentional reorienting. Looking at age group differences for error percentages as well as response times there was no congruency by age group interaction ($F_s < 1,840, p_s > .181$).

For response times there was a significant main effect of congruency for children, $F(1, 28) = 6,151, p < .05, \eta_p^2 = 0.180$ and a marginally significant one for adults, $F(1, 27) = 4,059, p = .054, \eta_p^2 = 0.131$. For both groups no congruency effects were found for error percentages ($F_s < 1,331, p_s > .259$).

A difference score on the response times was computed as a measure of incongruency cost during attentional reorienting (RT incongruent- RT congruent). Larger scores indicated greater incongruency cost. There was no significant relation between attentional reorienting and the EEB for children ($r = -.129$, $p = .503$) or for adults ($r = .134$, $p = .495$). There was also no relation between attentional reorienting and the EEB over the total sample, $r = -.031$, $p = .822$.

Processing speed. Looking at age group differences results revealed a significant main effect of age group, $F(1, 51) = 13,492$, $p < .01$, $\eta_p^2 = 0.213$ but no significant condition by group interaction, $F(1, 51) = 0,185$, $p = .669$, $\eta_p^2 = 0.004$. There was a significant main effect of condition for children, $F(1, 23) = 59,025$, $p < .001$, $\eta_p^2 = 0.729$ and adults, $F(1, 28) = 637,761$, $p < .001$, $\eta_p^2 = 0.958$. These results indicated as expected that for the four-choice the RTs were significantly larger for children as well adults.

A reaction time average of the one-choice and the four-choice reaction time task was computed and as a general measure of processing speed. There was a significant relation between processing speed and EEB for adults ($r = .424$, $p = .022$) no such relationship for children ($r = .104$, $p = .629$) but a significant relation between processing speed and the EEB over the total sample, $r = .310$, $p = .024$.

Multiple Regression Analysis

To further investigate which of the cognitive and affective measures uniquely account for individual differences in the EEB we performed a stepwise multiple regression over the total sample including all cognitive and affective measures. The result indicated that conflict processing significantly predicted the EEB crucially explaining a unique variance of the size in EEB ($F(1, 50) = 6,491$, $p < .05$, adjusted R square = .342).

Mediation Analysis

To investigate whether the observed developmental effects in EEB could be accounted for by age-related differences in other cognitive functions we performed a mediation analysis. According to Baron and Kenny (1986) three criteria have to be fulfilled for a mediation analysis: 1) the causal variable (in this case age group) has to be related with the outcome (in this case the EEB), 2) The causal variable has to correlate with the mediator, 3) the mediator has to have a effect on the outcome variable. Having tested 7 additional tasks to investigate possible associations between different cognitive functions and the EEB, we first corrected for multiple comparisons using a Bonferroni correction. Conflict processing emerged as the only other cognitive function that demonstrated robust differences between age groups, as well as a significant correlation with the EEB, that survived at the new alpha level of $p = .0071$. We therefore tested whether the observed age effects in the EEB would be mediated by differences in conflict processing. To do so, we conducted a mediation analysis where age was the predictor, conflict processing (error percentage) the mediator and EEB the outcome variable. Analyses were conducted using bootstrapping procedures recommended for smaller samples and dichotomous predictor variables (in this case age group) and operationalized in an SPSS Macro (Preacher & Hayes, 2008). We used 5,000 bootstrap resamples of the data with replacement. Statistical significance with alpha at .05 is indicated by the 95% confidence intervals not crossing zero.

We found a significant mediation effect of conflict processing with respect to the relationship between age and the EEB (indirect effect = 1.69, SE = 1.04, 95% confidence intervals = .23, 4.16) (see Figure 2.3). In addition this mediation was total, meaning that children's ability to solve conflict accounted solely for the age differences, as the direct effect of age did not significantly predict the EEB.

Mediation Model for the Effect of Age on EEB via Conflict Processing

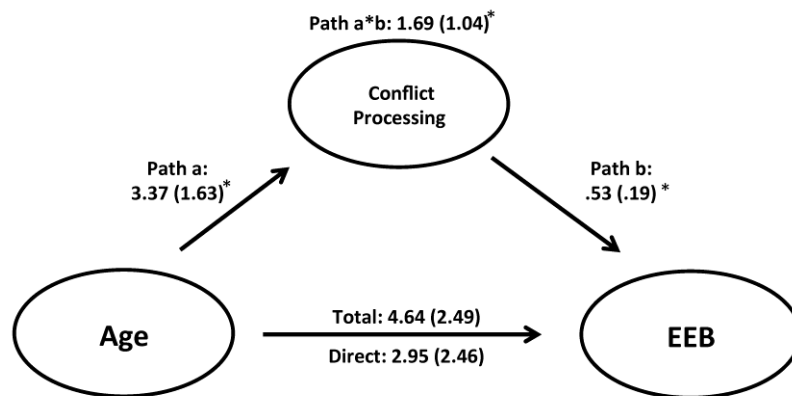


Figure 2.3. Display of the mediation model with emotional egocentricity bias as outcome variable, age as independent variable, and conflict processing as mediator variable. Values are unstandardized regression coefficients, and asterisks indicate significant coefficients (* $p < 0.05$). There was a significant mediation effect of conflict processing with respect to the relationship between age and the EEB.

Discussion

By using the novel ETAP based on visuo-gustatory stimulation to induce EEB, this study investigated developmental differences in the EEB between children and adults and their underlying cognitive mechanism. As compared to previous studies using either a visuo-touch (ETOP, Silani et al., 2013) or a monetary game paradigm (EMOP, Steinbeis et al., 2014) to induce EEB, using taste allowed us for the first time to elicit strong enough positive and negative emotions and thus a robust EEB in a children as well as adults with the same paradigm. Furthermore, the observed effects in adults as well as children were much larger than in previous studies (Silani et al., 2013; Steinbeis et al., 2014), which speak to the suitability of visuo-gustatory stimulation and the new ETAP for the investigation of the EEB. As hypothesized, children between the ages of 7 to 12 showed a significantly larger EEB

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compared to adults, which was double in size. Additionally, in line with previous findings (Steinbeis et al., 2014) the EEB decreased within the children sample from age 7 to 12. Developmental differences between children and adults were found in processing speed, visual perspective taking, inhibitory control and conflict processing but not for attentional reorienting and emotion regulation. Importantly, only conflict processing and none of the other cognitive and affective abilities showed a robust association with individual differences in the EEB. Indeed conflict processing was the only of the many cognitive and affective functions assessed that mediated the developmental differences observed in EEB between children and adults. This suggests that children's difficulty in overcoming the EEB seem to be best explained by their difficulties in conflict processing.

While conflicting information is both present, in the incongruent other as well as in the incongruent self condition of the ETAP, the response conflict is much larger when one has to take the perspective of another person which is incongruent to one's own than if you have to rate your own states even if these are incongruent to what the other is feeling. In the incongruent other condition the immediate emotional experience of the self seems to be more difficult to disregard than the more abstract notion of the other's emotional state conveyed by the picture in the incongruent self condition. Children's difficulties in conflict processing have been previously reported and it is assumed that conflict processing relevant brain regions such as the dorsal anterior cingulate cortex (dACC) and DLPFC develop throughout childhood into early adulthood (e.g. Fjell et al., 2012; Steinbeis et al., 2012). Though we have no direct evidence we propose that it is in particular the process of conflict resolution that plays a functional and critical role in overcoming emotional egocentricity. In support of this claim, the DLPFC in particular has been interpreted to play an important role in the resolution of conflict (Badre & Wagner, 2004; Chen, Wei, & Zhou, 2006; Egner & Hirsch, 2005; Kim, Kroger, & Kim, 2011), while also showing protracted maturation (Gogtay et al., 2004; Shaw et al., 2008; Sowell et al., 2003). Consequently the previously mentioned crucial involvement

of IDLPFC in overcoming EEB (Steinbeis et al., 2014), might be related to the underlying mechanism of conflict processing (resolution of conflict in particular), as identified in this study. It might be therefore suggested that IDLPFC communicates with rSMG, which disambiguates emotional self and other perspectives, and engages in conflict resolution to overcome emotional egocentricity bias to arrive at an accurate empathic judgment of the others' emotional state. Ongoing maturational processes in both, the IDLPFC and rSMG as well as their neuronal connections seem to make children more prone to an increased EEB compared to adults. It has to be noted that even though there is already some strong evidence to assume that a similar set of brain regions is recruited in the context of overcoming the EEB, whether this also holds for the present paradigm remains to be seen. Taken together, in ascribing the specific functional role of conflict resolution to IDLPFC in overcoming EEB, this study not only provides an underlying mechanism explaining age-related differences in EEB but also relates it to a specific neuronal architecture meaningfully tying together behavioural and neuroimaging findings. Even further, as empathic abilities have been linked to pro-social behaviours (Batson & Shaw, 1991; Eisenberg, 2000; Eisenberg et al., 1989; Hein et al., 2011; Hein et al., 2010), the identification of conflict processing as an underlying mechanism of developmental differences in EEB, could possibly inform targeted interventions leading to greater pro-sociality early in development by increasing the accuracy of empathic judgments in children.

In identifying conflict processing as an underlying mechanism of developmental differences in EEB, the question arises to what degree it is in particular children's ability to resolve an emotional conflict as compared to a non-emotional conflict during the ETOP. The conflict processing task in this study used emotional stimuli, so it can be argued that this task not only measures conflict processing per se but even beyond that measures emotional conflict processing. Previous research has shown that solving emotional conflicts versus non-emotional conflicts recruits very specific brain regions (Egner et al., 2008; Etkin et al., 2006).

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In the case of this study the emotional Go/NoGo task and non-emotional Go/NoGo task, while equivalent in design, did not correlate very highly ($r = .557$, $p < .001$) over the total sample, indicating that the affective aspects of the task are not totally accounted for by a general cognitive process. In sum, it can be argued that for children it might potentially be in particular their ability to resolve emotional conflicts that helps them to decrease their emotional egocentricity, however further research is needed too clarify this point, using emotional and non-emotional conflict processing tasks. In this study no significant compatibility effect was found for error rates in adults on the Flanker task. One plausible explanation could be a ceiling effect in performance, as adults are very good at resolving conflict, as also the low error rates for adults during incongruent trials in this study suggest.

Another important question of this study was whether egocentricity constitutes a unitary phenomenon in development and whether age-related changes in the extent of egocentricity undergo shared developmental trajectories. Interestingly, this study did not find any evidence for a relation between the EEB and visual perspective taking. Similarly to Theory of Mind, visual perspective taking has been associated with functioning of the rTPJ and not the rSMG (e.g. Ramsey et al., 2013). Visual perspective taking was investigated using a previously established paradigm (Surtees & Apperly, 2012) in order to search for possible commonalities with the EEB. Visual perspective taking, especially level-2 perspective taking has been found to be related to Theory of Mind (e.g. A. F. d. C. Hamilton, Brindley, & Frith, 2009) and as this paradigm also included a conflicting self and other perspectives it was very similar in demands to the ETAP and therefore a good comparison task. While developmental differences in visual perspective taking were indeed observed, with children committing more egocentric errors and showing higher incongruency-costs in reaction times as adults, these age-related differences were however unrelated to individual differences in the size of the EEB. This means that, for example, children showing egocentricity in visual perspective taking did not necessarily show such egocentricity in emotional perspective taking. This

finding together with the previous above mentioned findings (Silani et al., 2013; Steinbeis et al., 2014) supports the view that overcoming egocentricity in the emotional domain has to be seen as a different function than overcoming cognitive egocentricity involved in visual perspective taking and Theory of Mind tasks. This in turn suggests that egocentricity cannot be regarded as a unitary phenomenon in development, and future research should instead treat egocentricity as a phenomenon with considerable domain specificity.

Previous studies have suggested that the ability to overcome EEB is associated with brain functions of the rSMG (Silani et al., 2013; Steinbeis et al., 2014) and may be unrelated to abilities of attentional reorienting and Theory of Mind, both of which have been associated to functions of the adjacent rTPJ (Decety & Lamm, 2007; Mitchell, 2008; Scholz, Triantafyllou, Whitfield-Gabrieli, Brown, & Saxe, 2009). The present results are again a piece of evidence for such a functional segregation as again here the EEB was not related to attentional reorienting neither in children nor in adults. This suggests that the lower-level processes such as attentional reorienting, as well as processing speed are not crucially involved in overcoming emotional egocentricity, and do not explain any developmental differences in EEB.

Whereas conflict processing explained developmental differences in EEB, response inhibition as measured by the emotional and normal Go/NoGo task did not. This fact might be best explained by the nature of the EEB task. In contrast to false belief tasks and level 2 visual perspective taking tasks, which have been related to inhibitory control (Carlson & Moses, 2001; Friedman & Leslie, 2005; Perner & Lang, 1999; Wellman et al., 2001), mental states of self and other are not competing experiences, having the same object of reference but merely conflicting emotional experiences with differing objects of reference. So for example in a typical false belief task the two agents have different knowledge about where an object is hidden, while one agent's belief is necessarily true, the other agent's belief is necessarily false. In the EEB task in contrast the two agents have differing emotional experiences, each

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linked to a separate object of reference (e.g. juice vs quinine). While these emotional experiences are conflicting they are not competing realities as they remain true in their own right, bound to the individual experiences. Therefore, it can be hypothesized that response inhibition might be less involved in overcoming emotional egocentricity, as the emotional state of the self has to be disregarded rather than inhibited to arrive at a correct empathic judgment of the emotional state of the other. This would mean that conflicting emotional self and other representations are both online, but self representations do not have to be totally detached from to take the perspective of the other as in the case of false belief tasks. It might be specifically the ability selectively attend to one stimuli while ignoring the conflicting one which is presented simultaneously that distinguishes conflict processing from simple response inhibition, and relates conflict processing to overcoming emotional egocentricity during the ETOP. Additionally the blocked design used in this study minimized doubt about what the prepotent response should be (rating self or rating the other), therefore diminishing a further need for response inhibition. For future studies it would be interesting whether response inhibition would become increasingly involved, when using the ETOP with an even-related design.

Another cognitive capacity that has been hypothesized to potentially play a role in overcoming EEB and the developmental differences in EEB between children and adults, is emotion-regulation through cognitive reappraisal. To investigate children's and adults abilities to regulate their emotional states through cognitive reappraisal we developed an emotion regulation paradigm in which participants were instructed to regulate their taste experiences. This was done to closely match the emotion regulation task to the taste EEB task. Both children and adults were able to reappraise their taste experiences, and unlike our expectations and previous findings (e.g. McRae et al., 2012; Pitskel, Bolling, Kaiser, et al., 2011), no developmental differences in cognitive reappraisal emerged based on this task. It is unclear why no developmental differences were found. Albeit speculative it could be the case

that primary emotions are somehow easier to regulate than more complex secondary emotions. The significant association of conflict processing and age-related differences in the EEB might suggest that more basic and possibly more rapid cognitive processes might be involved in overcoming the EEB with its short time scale, leaving little room for more explicit and complex cognitive processes such as cognitive reappraisal.

Conclusion

Using a novel EEB paradigm based on visuo-gustatory stimulation, the ETAP, this study extends previous findings of the existence of an EEB in children and adults to another modality. Children between the ages of 7 to 12 exhibited a significantly larger EEB than adults. There was no evident link in the development of overcoming the EEB with developmental changes in cognitive egocentricity, speaking to egocentricity as a partly domain-specific phenomenon. In turn, the age-differences were mediated by conflict processing ability but not by a variety of other possibly relevant affective and cognitive abilities such as inhibition, attentional reorienting, processing speed or emotion regulation. Thus, the ability to process conflict seems to be crucial in overcoming emotional egocentricity bias and future research should aim to look more closely in what ways conflict processing and the EEB are interrelated on the behavioural and the neuronal level. Additionally, this study provided further evidence for the assumption that overcoming emotional egocentricity is independent of other functions also relying on temporo-parietal functions such as attentional reorienting, Theory of Mind and visual perspective taking. The further investigation of the EEB in development and its interrelation with the development of conflict processing in general seems of great significance, as inappropriate and egocentrically biased empathic judgments can hamper the normal development of interpersonal understanding, be the cause of conflicts and could lead to detrimental consequences for developing children trying to find their place in their social world. In this sense identifying underlying mechanisms of emotional egocentricity in development, such as conflict processing, can help to inform interventions

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promoting normative change in cases where children show great difficulties in overcoming emotional egocentricity.

References

- Apperly, I. A., Warren, F., Andrews, B. J., Grant, J., & Todd, S. (2011). Developmental continuity in theory of mind: Speed and accuracy of belief–desire reasoning in children and adults. *Child development*, 82(5), 1691-1703.
- Badre, D., & Wagner, A. D. (2004). Selection, integration, and conflict monitoring: assessing the nature and generality of prefrontal cognitive control mechanisms. *Neuron*, 41(3), 473-487.
- Baron, R. M., & Kenny, D. A. (1986). The moderator–mediator variable distinction in social psychological research: Conceptual, strategic, and statistical considerations. *Journal of personality and social psychology*, 51(6), 1173-1182.
- Batson, C. D., & Shaw, L. L. (1991). Evidence for altruism: Toward a pluralism of prosocial motives. *Psychological Inquiry*, 2(2), 107-122.
- Birch, S. A., & Bloom, P. (2007). The curse of knowledge in reasoning about false beliefs. *Psychological Science*, 18(5), 382-386.
- Carlson, S. M., & Moses, L. J. (2001). Individual differences in inhibitory control and children's theory of mind. *Child development*, 72(4), 1032-1053.
- Carter, R. M., & Huettel, S. A. (2013). A nexus model of the temporal–parietal junction. *Trends in cognitive sciences*, 17(7), 328-336.
- Chen, Q., Wei, P., & Zhou, X. (2006). Distinct neural correlates for resolving stroop conflict at inhibited and noninhibited locations in inhibition of return. *Journal of cognitive neuroscience*, 18(11), 1937-1946.
- Deary, I. J., Der, G., & Ford, G. (2001). Reaction times and intelligence differences: A population-based cohort study. *Intelligence*, 29(5), 389-399.

2. Manuscript of Study 1

- Decety, J., & Lamm, C. (2007). The role of the right temporoparietal junction in social interaction: how low-level computational processes contribute to meta-cognition. *The Neuroscientist*, 13(6), 580-593.
- Egner, T., Etkin, A., Gale, S., & Hirsch, J. (2008). Dissociable neural systems resolve conflict from emotional versus nonemotional distracters. *Cerebral Cortex*, 18(6), 1475-1484.
- Egner, T., & Hirsch, J. (2005). Cognitive control mechanisms resolve conflict through cortical amplification of task-relevant information. *Nature neuroscience*, 8(12), 1784-1790.
- Eisenberg, N. (2000). Emotion, regulation, and moral development. *Annual review of psychology*, 51(1), 665-697.
- Eisenberg, N., Fabes, R. A., Miller, P. A., Fultz, J., Shell, R., Mathy, R. M., & Reno, R. R. (1989). Relation of sympathy and personal distress to prosocial behavior: a multimethod study. *Journal of personality and social psychology*, 57(1), 55-66.
- Eisenberg, N., Shell, R., Pasternack, J., Lennon, R., Beller, R., & Mathy, R. M. (1987). Prosocial development in middle childhood: A longitudinal study. *Developmental psychology*, 23(5), 712-718.
- Eriksen, B. A., & Eriksen, C. W. (1974). Effects of noise letters upon the identification of a target letter in a nonsearch task. *Perception & psychophysics*, 16(1), 143-149.
- Etkin, A., Egner, T., Peraza, D. M., Kandel, E. R., & Hirsch, J. (2006). Resolving emotional conflict: a role for the rostral anterior cingulate cortex in modulating activity in the amygdala. *Neuron*, 51(6), 871-882.
- Fenske, M. J., & Eastwood, J. D. (2003). Modulation of focused attention by faces expressing emotion: evidence from flanker tasks. *Emotion*, 3(4), 327-343.
- Fjell, A. M., Walhovd, K. B., Brown, T. T., Kuperman, J. M., Chung, Y., Hagler, D. J., . . . McCabe, C. (2012). Multimodal imaging of the self-regulating developing brain. *Proceedings of the National Academy of Sciences*, 109(48), 19620-19625.

- Flavell, J. H., Everett, B. A., Croft, K., & Flavell, E. R. (1981). Young children's knowledge about visual perception: Further evidence for the Level 1–Level 2 distinction. *Developmental psychology*, 17(1), 99-103.
- Friedman, O., & Leslie, A. M. (2005). Processing demands in belief-desire reasoning: inhibition or general difficulty? *Developmental Science*, 8(3), 218-225.
- Gogtay, N., Giedd, J. N., Lusk, L., Hayashi, K. M., Greenstein, D., Vaituzis, A. C., . . . Toga, A. W. (2004). Dynamic mapping of human cortical development during childhood through early adulthood. *Proceedings of the National Academy of Sciences of the United States of America*, 101(21), 8174-8179.
- Green, B. G., Dalton, P., Cowart, B., Shaffer, G., Rankin, K., & Higgins, J. (1996). Evaluating the ‘Labeled Magnitude Scale’ for measuring sensations of taste and smell. *Chemical Senses*, 21(3), 323-334.
- Gross, J. J. (2002). Emotion regulation: Affective, cognitive, and social consequences. *Psychophysiology*, 39(3), 281-291.
- Hamilton, A. F. d. C., Brindley, R., & Frith, U. (2009). Visual perspective taking impairment in children with autistic spectrum disorder. *Cognition*, 113(1), 37-44.
- Hansen Lagattuta, K., Sayfan, L., & Harvey, C. (2013). Beliefs About Thought Probability: Evidence for Persistent Errors in Mindreading and Links to Executive Control. *Child development*, 85(2), 659-674.
- Hare, T. A., Tottenham, N., Galvan, A., Voss, H. U., Glover, G. H., & Casey, B. (2008). Biological substrates of emotional reactivity and regulation in adolescence during an emotional go-nogo task. *Biological psychiatry*, 63(10), 927-934.
- Hein, G., Lamm, C., Brodbeck, C., & Singer, T. (2011). Skin conductance response to the pain of others predicts later costly helping. *PloS one*, 6(8), e22759.

2. Manuscript of Study 1

- Hein, G., Silani, G., Preuschoff, K., Batson, C. D., & Singer, T. (2010). Neural responses to ingroup and outgroup members' suffering predict individual differences in costly helping. *Neuron*, 68(1), 149-160.
- Jabbi, M., Swart, M., & Keysers, C. (2007). Empathy for positive and negative emotions in the gustatory cortex. *Neuroimage*, 34(4), 1744-1753.
- Kail, R. (1991). Developmental change in speed of processing during childhood and adolescence. *Psychological bulletin*, 109(3), 490-501.
- Keysar, B., Lin, S., & Barr, D. J. (2003). Limits on theory of mind use in adults. *Cognition*, 89(1), 25-41.
- Kim, C., Kroger, J. K., & Kim, J. (2011). A functional dissociation of conflict processing within anterior cingulate cortex. *Human brain mapping*, 32(2), 304-312.
- Li, S.-C., Lindenberger, U., Hommel, B., Aschersleben, G., Prinz, W., & Baltes, P. B. (2004). Transformations in the couplings among intellectual abilities and constituent cognitive processes across the life span. *Psychological Science*, 15(3), 155-163.
- Luna, B., Garver, K. E., Urban, T. A., Lazar, N. A., & Sweeney, J. A. (2004). Maturation of cognitive processes from late childhood to adulthood. *Child development*, 75(5), 1357-1372.
- Mars, R. B., Sallet, J., Schüffelgen, U., Jbabdi, S., Toni, I., & Rushworth, M. F. (2012). Connectivity-based subdivisions of the human right “temporoparietal junction area”: evidence for different areas participating in different cortical networks. *Cerebral Cortex*, 22(8), 1894-1903.
- McRae, K., Gross, J. J., Weber, J., Robertson, E. R., Sokol-Hessner, P., Ray, R. D., . . . Ochsner, K. N. (2012). The development of emotion regulation: an fMRI study of cognitive reappraisal in children, adolescents and young adults. *Social Cognitive and Affective Neuroscience*, 7(1), 11-22.

- Mitchell, J. P. (2008). Activity in right temporo-parietal junction is not selective for theory-of-mind. *Cerebral Cortex*, 18(2), 262-271.
- Mitchell, J. P. (2009). Inferences about mental states. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1521), 1309-1316.
- Moll, H., & Tomasello, M. (2006). Level 1 perspective-taking at 24 months of age. *British Journal of Developmental Psychology*, 24(3), 603-613.
- Newcomb, A. F., Bukowski, W. M., & Pattee, L. (1993). Children's peer relations: a meta-analytic review of popular, rejected, neglected, controversial, and average sociometric status. *Psychological bulletin*, 113(1), 99-128.
- Nickerson, R. S. (2001). The projective way of knowing: A useful heuristic that sometimes misleads. *Current Directions in Psychological Science*, 10(5), 168-172.
- O'doherty, J., Rolls, E., Francis, S., Bowtell, R., & McGlone, F. (2001). Representation of pleasant and aversive taste in the human brain. *Journal of neurophysiology*, 85(3), 1315-1321.
- O'Brien, E., & Ellsworth, P. C. (2012). More Than Skin Deep Visceral States Are Not Projected Onto Dissimilar Others. *Psychological Science*, 23(4), 391-396.
- Perner, J., & Lang, B. (1999). Development of theory of mind and executive control. *Trends in cognitive sciences*, 3(9), 337-344.
- Piaget, J., & Inhelder, B. (1956). *The Child's Conception of Space*. London: Routledge & Kegan Paul
- Pitskel, N. B., Bolling, D. Z., Kaiser, M. D., Crowley, M. J., & Pelphrey, K. A. (2011). How grossed out are you? The neural bases of emotion regulation from childhood to adolescence. *Developmental cognitive neuroscience*, 1(3), 324-337.
- Preacher, K. J., & Hayes, A. F. (2008). Asymptotic and resampling strategies for assessing and comparing indirect effects in multiple mediator models. *Behavior research methods*, 40(3), 879-891.

2. Manuscript of Study 1

- Pronin, E. (2008). How we see ourselves and how we see others. *Science*, 320(5880), 1177-1180.
- Ramsey, R., Hansen, P., Apperly, I., & Samson, D. (2013). Seeing it my way or your way: Frontoparietal brain areas sustain viewpoint-independent perspective selection processes. *Journal of cognitive neuroscience*, 25(5), 670-684.
- Repacholi, B. M., & Gopnik, A. (1997). Early reasoning about desires: evidence from 14-and 18-month-olds. *Developmental psychology*, 33(1), 12-21.
- Royzman, E. B., Cassidy, K. W., & Baron, J. (2003). " I know, you know": Epistemic egocentrism in children and adults. *Review of General Psychology*, 7(1), 38-65.
- Scholz, J., Triantafyllou, C., Whitfield-Gabrieli, S., Brown, E. N., & Saxe, R. (2009). Distinct regions of right temporo-parietal junction are selective for theory of mind and exogenous attention. *PloS one*, 4(3), e4869.
- Shaw, P., Kabani, N. J., Lerch, J. P., Eckstrand, K., Lenroot, R., Gogtay, N., . . . Rapoport, J. L. (2008). Neurodevelopmental trajectories of the human cerebral cortex. *The Journal of Neuroscience*, 28(14), 3586-3594.
- Silani, G., Lamm, C., Ruff, C. C., & Singer, T. (2013). Right Supramarginal Gyrus Is Crucial to Overcome Emotional Egocentricity Bias in Social Judgments. *The Journal of Neuroscience*, 33(39), 15466-15476.
- Small, D. M., Gregory, M. D., Mak, Y. E., Gitelman, D., Mesulam, M., & Parrish, T. (2003). Dissociation of neural representation of intensity and affective valuation in human gustation. *Neuron*, 39(4), 701-711.
- Sommerville, J. A., Bernstein, D. M., & Meltzoff, A. N. (2013). Measuring Beliefs in Centimeters: Private Knowledge Biases Preschoolers' and Adults' Representation of Others' Beliefs. *Child development*, 84(6), 1846-1854.

- Sowell, E. R., Peterson, B. S., Thompson, P. M., Welcome, S. E., Henkenius, A. L., & Toga, A. W. (2003). Mapping cortical change across the human life span. *Nature neuroscience*, 6(3), 309-315.
- Steinbeis, N., Bernhardt, B. C., & Singer, T. (2012). Impulse control and underlying functions of the left DLPFC mediate age-related and age-independent individual differences in strategic social behavior. *Neuron*, 73(5), 1040-1051.
- Steinbeis, N., Bernhardt, B. C., & Singer, T. (2014). Age-related Differences in Function and Structure of rSMG and Reduced Functional Connectivity with DLPFC Explains Heightened Affective Egocentricity Bias in Childhood. *Social Cognitive and Affective Neuroscience*. nsu057.
- Surtees, A. D., & Apperly, I. A. (2012). Egocentrism and automatic perspective taking in children and adults. *Child development*, 83(2), 452-460.
- Thomas, R. C., & Jacoby, L. L. (2012). Diminishing adult egocentrism when estimating what others know. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 39(2), 473-486.
- Thompson, L., & Loewenstein, G. (1992). Egocentric interpretations of fairness and interpersonal conflict. *Organizational Behavior and Human Decision Processes*, 51(2), 176-197.
- Tottenham, N., Tanaka, J. W., Leon, A. C., McCarry, T., Nurse, M., Hare, T. A., . . . Nelson, C. (2009). The NimStim set of facial expressions: judgments from untrained research participants. *Psychiatry research*, 168(3), 242-249.
- Van Boven, L., & Loewenstein, G. (2003). Social projection of transient drive states. *Personality and Social Psychology Bulletin*, 29(9), 1159-1168.
- Wellman, H. M., Cross, D., & Watson, J. (2001). Meta-analysis of theory-of-mind development: the truth about false belief. *Child development*, 72(3), 655-684.

2. Manuscript of Study 1

- Williams, B. R., Ponesse, J. S., Schachar, R. J., Logan, G. D., & Tannock, R. (1999). Development of inhibitory control across the life span. *Developmental psychology*, 35(1), 205-213.
- Wimmer, H., & Perner, J. (1983). Beliefs about beliefs: Representation and constraining function of wrong beliefs in young children's understanding of deception. *Cognition*, 13(1), 103-128.

3. Manuscript of Study 2

Preserved self-other distinction during empathy in autism is linked to network integrity of right supramarginal gyrus

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Abstract

Background

Autism Spectrum Disorder (ASD) shows known deficits in self-other distinction during Theory of Mind (ToM). Whether self-other distinction during empathy is deficient in ASD remains unknown.

Aims

To investigate whether ASD patients show difficulties in emotional self-other distinction as mirrored in increased emotional egocentricity and if potential deficits are linked to dysfunctional resting-state connectivity patterns.

Methods

In a first study, ASD patients and matched controls performed an emotional egocentricity paradigm and a ToM task. In the second study, resting-state connectivity of right temporoparietal junction (rTPJ) and right supramarginal gyrus (rSMG) were analysed using a large-scale fMRI data set.

Results

ASD patients exhibited deficient ToM but normal emotional egocentricity, which was paralleled by reduced connectivity of regions of the ToM network and unimpaired rSMG network connectivity.

Conclusions

Results suggest normal emotional egocentricity and intact rSMG network in ASD, indicating spared self-other distinction during empathy in patients stigmatized to suffer from broad social deficits.

Declaration of interest

None.

Introduction

Autism spectrum disorder (ASD) is a common, early-onset neurodevelopmental disorder characterized by impairments in social communication, interaction, and stereotyped or repetitive behaviours and interests (American Psychiatric Association, 2013). Already in his original paper, Asperger (1944) described the children he studied as being “egocentric to the extreme”. Consequently, one of the most consistently reported social cognition deficits in ASD has been in Theory of Mind (ToM) (Baron-Cohen et al., 1985; Castelli et al., 2002; Frith & Frith, 2012; Happé, 1994) the socio-cognitive ability to understand the mental states of others, such as beliefs and intentions (Premack & Woodruff, 1978). When engaging in ToM tasks, higher egocentrism of individuals with ASD compared to non-autistic individuals is for example evidenced by their increased difficulty in passing false belief tasks (Baron-Cohen et al., 1985; Begeer et al., 2012; Senju et al., 2010; Senju et al., 2009).

It has been proposed that the underlying problem in ToM and in particular false belief understanding for individuals with ASD is difficulties in differentiating between perspectives of self and other, also known as self-other distinction (Lombardo & Baron-Cohen, 2011). Human interpersonal understanding often relies on mechanisms of self-projection and simulation (Bastiaansen, Thioux, & Keysers, 2009; Brass et al., 2009; Decety & Lamm, 2007; Gallese, 2001, 2007; Gallese & Goldman, 1998; Mitchell, 2009; Nickerson, 2001; Silani et al., 2013; Singer, 2012; Singer et al., 2004; Steinbeis et al., 2014; Van Boven & Loewenstein, 2003). However, such projection mechanisms fail in making sense of other’s mental states in situations where mental states of self and other clearly differ, such as in typical false belief tasks, eventually leading to egocentrically biased judgments (Birch & Bloom, 2007; Pronin, 2008; Royzman et al., 2003). To avoid egocentrically biased judgments, a mechanism differentiating between self and other perspectives has to be in place. In sum, context

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appropriate differentiation of self and other might be at the core of many social cognition deficits displayed in ASD.

While self-other distinction during ToM seems to be crucial, recent evidence has shown that self-other distinction is of equal importance during empathic relating (Silani et al., 2013; Steinbeis et al., 2014). Empathy involves sharing the emotional state of others while being aware that the other is the source of that state (Singer & Lamm, 2009), requiring emotional self-other distinction particularly in cases, where emotional states of self and other are incongruent. Failure of self-other distinction during empathy results in egocentric emotional responses, e.g. failure to share sadness of a friend when being in a good mood. While deficits in ToM in ASD have been consistently reported, it remains less clear whether individuals with ASD also have difficulties in empathy, particularly when emotional states between oneself and others might differ in valence. There is indeed good evidence that empathy may be intact in ASD (Hadjikhani et al., 2014; Jones et al., 2010; Lockwood et al., 2013; Rogers, Dziobek, Hassenstab, Wolf, & Convit, 2007). While some studies have reported lower empathy in ASD (Bird et al., 2010; Dapretto et al., 2005; Minio-Paluello, Baron-Cohen, Avenanti, Walsh, & Aglioti, 2009), there is increasing evidence that such deficits might arise more from comorbid alexithymia, i.e. inability to identify and describe one's own emotions, as opposed to autism-specific deficits per se (Bird & Cook, 2013). As empathy might thus be intact in ASD, it is still an open question if, in case of incongruent emotional states, individuals with ASD would display increased emotional egocentricity, indicating poor self-other distinction also in the affective domain. Our main aim was therefore to test for increased emotional egocentricity bias (EEB) in ASD compared to normal controls. In this study we used the EEB Touch-Paradigm (ETOP) (Silani et al., 2013), in which emotions are induced via tactile stimulation. The ETOP allows to measure pure empathic relating under different conditions, when emotional states of self and other are congruent or

incongruent, thus assessing empathic simulation, but also self-other distinction during empathy.

A key brain region adequately suited for self-other distinction in the cognitive domain, being a hub of both interoceptive and exteroceptive information pathways is the so-called temporo-parietal junction (TPJ). TPJ has shown to be consistently recruited during ToM (Aichhorn et al., 2006; Decety & Lamm, 2007; Ramsey et al., 2013; Sommer et al., 2007). In particular the right TPJ, has been suggested to play a major role during ToM, especially when self-other distinction is required (Aichhorn et al., 2006; Sommer et al., 2007). It has however been suggested that rTPJ plays a more general role in self-other distinction in the cognitive as well as motor domain, based on results from meta analyses and single studies, showing a relation between the inhibition of spontaneous imitation tendencies (i.e. self-other distinction in the motor domain) and ToM abilities (Santesteban, White, et al., 2012; Spengler et al., 2009, 2010). A recent study using transcranial direct current stimulation (tDCS) of rTPJ provided strong evidence that rTPJ is causally involved in differentiating self and other during imitation inhibition and ToM (Santesteban, Banissy, et al., 2012). Thus rTPJ might help to differentiate self and other perspectives during ToM but also in the motor domain. In the case of ASD, structural and functional abnormalities of rTPJ have been linked to social cognition deficits. Conversely, recent research that self-other distinction in the emotional domain may be subserved by brain regions part of temporo-parietal cortex, but slightly more anterior to TPJ, namely the right supramarginal gyrus (rSMG). Thus, a study by Silani et al. (2013) demonstrated that adults show an emotional egocentricity bias (EEB) when judging the emotional state of another person incongruent to their own, while the right supramarginal gyrus (rSMG) was functionally implicated in overcoming EEB. Peaks of this activation were distinct from other subregions of temporo-parietal cortex involved in ToM. In line with these findings, a study by Steinbeis et al. (2014) showed that children displayed increased emotional egocentricity compared to adults related to reduced activation of rSMG. In a

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complementary resting-state connectivity analysis, rSMG showed stronger functional connectivity to regions of the empathy network, such as the middle cingulate cortex, bilateral anterior insulae (AI), extending to inferior frontal gyrus (IFG) and bilateral dorsolateral prefrontal cortex (DLPFC), while rTPJ showed stronger functional connectivity to nodes of the ToM network, including the medial prefrontal cortex (MPFC) and the precuneus. Taken together these findings corroborate the hypothesis that the broader area usually referred to as temporal parietal cortex consists of important subdivisions that in turn might subserve different functions in the context of social cognition respectively such as self-other distinction during empathy on the one hand as compared to ToM on the other. A second aim of the present study was to test for differences in the associated brain regions supporting the function of overcoming emotional egocentricity on the one hand and ToM on the other hand. In order to do so we analyzed resting-state functional connectivity data in an independent large multi-center sample of individuals with ASD and matched healthy controls, seeding from rSMG, a region directly implicated in overcoming emotional egocentricity and rTPJ, a region commonly shown to play a crucial role during ToM.

To sum up we aimed to investigate whether individuals with ASD relative to healthy controls would show normal emotional egocentricity, differentiating self and other perspective during empathic relating, associated with intact functioning of the rSMG-related brain network. In contrast we hypothesized that individuals with ASD relative to healthy controls would exhibit known deficits in ToM possibly linked to problems differentiating self and other perspectives in the cognitive domain related to aberrant functioning of the rTPJ-related brain network.

Methods

Participants

Behavioural sample. For Study 1, 32 adults with ASD and 26 healthy controls were recruited. In the case of the ASD patients 4 participants showed abnormal emotional responses to the stimuli (e.g. rated positive stimuli as negative and vice versa) and were excluded from further analysis. 3 ASD patients and 1 healthy control participants were later excluded, showing abnormal emotional egocentricity, with ratings above two standard deviations. Subsequently the final sample included 25 adults with ASD and 25 IQ and gender-matched neurotypical participants (see Table 3.1). ASD participants were recruited through the outpatient clinic of the Charité University Medicine Berlin, or were referred to us by specialized clinicians. Diagnoses according to DSM-IV criteria (American Psychiatric Association, 2000) for Asperger disorder and autistic disorder without intellectual disabilities were based on expert clinical opinion and the Autism Diagnostic Observation Schedule, ADOS (Lord et al., 2000), and the Autism Diagnostic Interview-Revised (ADI-R), if parental information was available ($n = 14$). ADOS - scores are used as a measure for symptom severity throughout this article. Healthy control (HC) participants with no history of psychiatric or neurological disorders were recruited by public notices and from project databases of the Freie Universität Berlin and the Max Planck Institute for Human Cognitive and Brain Sciences Leipzig, Germany. Crystalline and fluid intelligence levels were estimated by means of a verbal intelligence (German vocabulary test / Mehrfach-Wortschatz-Test (MWT), Lehrl, Triebig, & Fischer, 1995) and a strategic thinking test (LPS, subscale 4, Horn, 1962) respectively, and combined to yield a full scale IQ (FIQ). Autistic traits and Alexithymia were assessed in both groups using the Autism Quotient and the Toronto Alexithymia Scale (TAS-26, Taylor, Ryan, & Bagby, 1985), respectively. Participants gave informed consent prior to participation and received payment. The study was approved by the ethics committee of the German Society for Psychology (DGPs).

Table 3.1. Demographic characteristics and diagnosis of the behavioural sample (Study 1)

Behavioural sample	ASD	HC	ASD vs. HC
	M (SD)	M (SD)	
Sample size	25	25	
Gender	18 males	18 males	
Age	32.6 (8.5)	32.4 (8.5)	$p = .960$
Full IQ	115.8 (9.1)	112.8 (8.0)	$p = .246$
AQ	36.9 (8.0)	13.7 (4.7)	$p < .001^{***}$
TAS-26	54.2 (10.0)	37.4 (7.8)	$p < .001^{***}$
ADOS	11.0 (3.8)		

Statistics applied: independent t-test. * $p < .05$, ** $p < .01$, *** $p < .001$.

Imaging sample. For Study 2, we studied a subsample of 163 (84 ASDs, 79 healthy controls) male participants from the Autism Brain Imaging Data Exchange (ABIDE) database, a publically available multi-center aggregate of previously collected structural and functional MRI data from individuals with ASD and healthy controls (see http://fcon_1000.projects.nitric.org/indi/abide and Supplement 1). ASD diagnosis according to DSM-IV criteria (American Psychiatric Association, 2000) were based on expert clinical opinion and the Autism Diagnostic Observation Schedule, ADOS ($n = 63$) (Lord et al., 2000), and/or the Autism Diagnostic Interview-Revised, ADI-R ($n = 27$) (Lord, Rutter, & Le Couteur, 1994). Note that for the individuals of the behavioural sample no resting-state scans were available. To further inform the behavioural results, however, we chose to analyze resting-state data from the ABIDE database. The selected sample (see Table 3.2, see also supplemental material) was chosen to be within the same age range as the behavioural sample

(20-55 years), and ASD participants of both samples did not differ in terms of symptom severity as measured through the ADOS. Within the imaging sample, individuals with ASD only differed in terms of full scale IQ to the healthy controls. Subsequently, full scale IQ was used as a covariate of no interest in the resting-state analysis.

Table 3.2. Demographic characteristics and diagnosis of the fMRI sample (Study 2)

fMRI sample	ASD	HC	ASD vs. HC
	M (SD)	M (SD)	
Sample size	78	77	
Gender	all males	all males	
Age	25.4 (6.9)	25.5 (6.1)	$p = .956$
Full IQ	108.1 (16.3)	115.6 (11.9)	$p = .001^{**}$
ADOS (N = 63)	12.6 (3.9)		

Statistics applied: independent t-test. * $p < .05$, ** $p < .01$, *** $p < .001$.

EEB Touch-Paradigm (ETOP)

The design and procedure of this paradigm was identical to that reported in Silani et al. (2013) and is described in further detail in Supplement 1. Participants were invited pairwise to an experimental session and while sitting back-to-back were asked to rate on a touch screen the pleasantness or unpleasantness of tactile stimulation of their left palm. In the crucial simultaneous conditions of this task, both participants received tactile stimulation simultaneously, and were instructed to either judge the pleasantness of their own tactile experience (simultaneous self condition) or judge the pleasantness of the tactile experience for the other person (simultaneous other condition). In these conditions two pictures appeared on

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the screen, while the left picture with the label “Self” corresponded to the tactile stimulation the participant received (e.g. a picture of a rose while the participant was touched by a silky object), the right picture with the label “Other” corresponded to the touch the other person received. The touch experiences of the two participants could be either affectively congruent (e.g. both touched by pleasant materials, e.g. silk and fur) or incongruent (e.g. one gets touched by a pleasant, the other by an unpleasant material, e.g. silk and rubber spider). Immediately after the stimulation phase (3000 ms) participants judged the pleasantness or unpleasantness of the tactile experience using a rating scale ranging from -10 to 10 on the touch screen within 3000 ms response time. The EEB was defined as the difference between ratings in incongruent and congruent trials when judging the other, as compared to the difference when judging one’s own feelings.

To assess whether emotion induction worked for both groups, each session started with individual conditions, in which participants received tactile stimulation one-by-one instructed to either judge the pleasantness of their own touch stimulation or the pleasantness of the tactile stimulation for the other person based on the picture indicating what tactile stimulation the other participant received (see Supplement 1).

Movie for the Assessment of Social Cognition (MASC)

During the MASC participants are watching a 15 min movie about four characters spending an evening together, which is stopped 45 times for questions about the actors' mental states. Correct responses were computed to a total score. The MASC has proven internal consistency, sensitivity, stability over time (Dziobek et al., 2006) and has been used with different patient populations (Montag et al., 2011; Montag et al., 2010; Ritter et al., 2011).

Resting-state connectivity analysis

Data were processed using the data processing assistant for the resting-state fMRI toolbox (DPARSF, Song et al., 2011) for Matlab. The toolbox is based on the Statistical Parametric Mapping toolbox (SPM8, <http://www.fil.ion.ucl.ac.uk/spm>). Preprocessing followed a standard procedure, including a scrubbing approach and a band-filter within the 0.01 and 0.08 Hz band (Satterthwaite et al., 2013), to deal more thoroughly with motion artifacts. Images underwent DARTEL-based segmentation and registration, followed by nuisance covariate regression to remove effects of average WM and CSF signal, as well as 6 motion parameters (For further details of the data preprocessing and connectivity analyses please refer to Supplement 1). In the resting-state sample, 6/84 individuals with ASD and 2/79 of healthy controls showed head-motion beyond 3mm translation or 3 degrees of rotation and were excluded from all further analysis. Functional connectivity maps were generated for both rSMG and rTPJ, based on the overlap of activations from two separate fMRI experiments using the ETOP ($MNI_{xyz} = 65, -37, 33$) and a coordinate-based meta-analysis of rTPJ-activation in ToM studies by Mar (2011) respectively ($MNI_{xyz} = 51, -52, 21$). Results of this analysis were provided as a NIfTI File thresholded at $p = 0.01$, FDR-corrected. Both regions the rSMG and rTPJ region were adjacent to each other but spatially non-overlapping (Figure 3.1). Group differences in functional connectivity were analyzed with SPM8 using random-effects models, assessing interactions between within-subject difference of rTPJ to rSMG connectivity and the group. For ASD patients whole-brain correlations were run using the ADOS social score, as a measure of symptom severity. The number of sites, age and FIQ were included in the model as covariates of no interest. Using Monte Carlo simulation correcting for multiple comparison cluster size corrected results are reported (voxel-wise p value of .01 combined with an extent threshold of 77 voxels corresponded to cluster-wise family-wise error rate of .05).

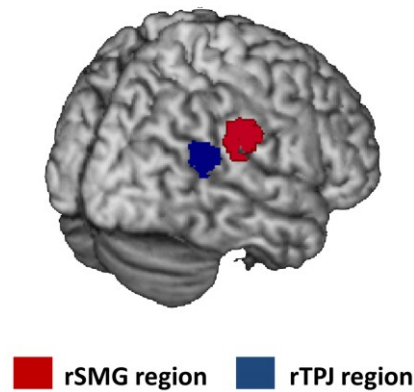


Figure 3.1. Display of adjacent but non-overlapping rSMG and rTPJ regions used for functional connectivity analysis in a large independent sample of individuals with ASD and healthy controls. The rSMG region consists of an overlap of activations of two fMRI experiments ($MNI_{xyz} = 65, -37, 33$) looking at the neuronal basis of the EEB using the ETOP (Silani et al., 2013). The rTPJ region ($MNI_{xyz} = 51, -52, 21$) was taken from a meta-analytic activation during ToM (Mar, 2011).

Results

EEB Touch-Paradigm (ETOP)

Simultaneous conditions. To investigate whether ASD participants and healthy controls display different emotional egocentricity an ANOVA on the affective ratings with target, congruency and valence as within-subjects factors and group as between-subjects factor was performed.

The results showed significant main effects of target ($F_{1,48} = 11.14, p = .002, \eta_p^2 = .188$), valence ($F_{1,48} = 16.92, p < .001, \eta_p^2 = .261$), and group ($F_{1,48} = 6.10, p = .013, \eta_p^2 = .113$), and significant interactions of target and valence ($F_{1,48} = 9.57, p = .003, \eta_p^2 = .166$), and congruency, valence and group ($F_{1,48} = 4.70, p = .035, \eta_p^2 = .089$). Importantly however, while there was a significant target by congruency interaction ($F_{1,48} = 10.58, p = .002, \eta_p^2 =$

.181), there was no significant interaction of target, congruency and group, suggesting no group difference in emotional egocentricity ($F_{1,48} = 0.17, p = .684, \eta_p^2 = .003$). Both ASD participants and healthy controls however showed a significant EEB ($F_{1,24} = 5.56, p = .027, \eta_p^2 = .188$; $F_{1,24} = 5.27, p = .031, \eta_p^2 = .180$). Including the TAS score as a covariate in the model revealed no significant interaction of target, congruency and group ($F_{1,48} = 0.02, p = .882, \eta_p^2 = .00047$), ruling out that any possible differences in EEB between healthy controls and ASD participants was being masked by alexithymia in the ASD group. In fact, the EEB of ASD participants and healthy controls was comparable in size ($t_{48} = 0.41, p = .684, 95\% CI = -.40 \leq \mu_1 - \mu_2 \leq .60, d = .11, 95\% CI = -0.44 \leq \Delta \leq 0.67$) (ASD = 0.35, Healthy controls = 0.45, Figure 3.2A). The EEB in ASD participants was unrelated to symptom severity ($r = -.20, p = .365$) (for the results of the individual conditions see Supplement 1).

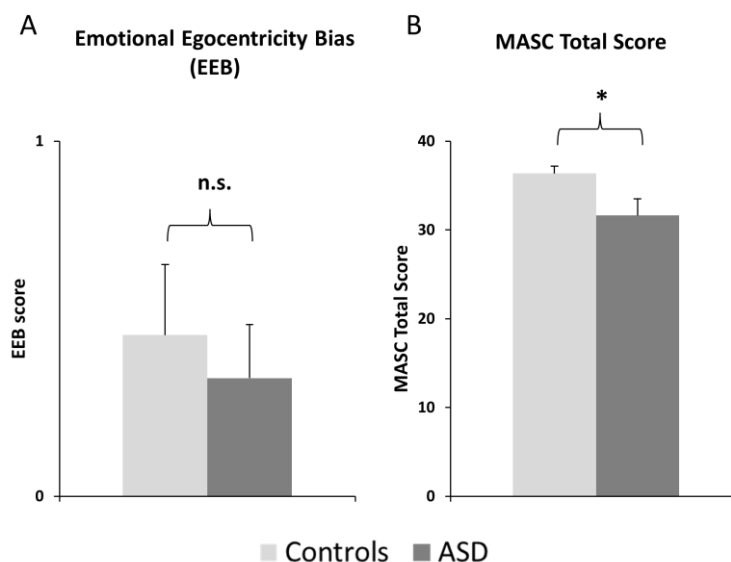


Figure 3.2. (A) Display of the Emotional Egocentricity Bias (EEB). Both groups displayed a significant EEB but the size of the EEB was similar for individuals with ASD and healthy controls, suggesting intact self-other distinction during empathic relating in ASD. (B) MASC Total Score. As expected healthy controls showed a significantly greater MASC score than individuals with ASD, suggesting deficient ToM in ASD.

Movie for the Assessment of Social Cognition (MASC)

ASD participants showed significantly lower scores on the MASC ($t_{46} = 2.32$, $p = .025$; Figure 3.2B) Scores on the MASC were negatively related to symptom severity as measured by the ADOS ($r = -.69$, $p = .001$). Additionally the MASC score were unrelated to the EEB for ASD patients ($r = .10$, $p = .648$) and healthy controls ($r = -.08$, $p = .712$).

Resting-state connectivity analysis

We directly compared the voxel-wise connectivity strength of both regions within subjects combining individuals with ASD and healthy controls. The rSMG showed marked connectivity patterns relative to rTPJ to the lSMG, the bilateral AI extending into IFG, the medial cingulate cortex (MCC) and bilateral dorsal lateral prefrontal cortex (DLPFC). In contrast rTPJ showed significantly stronger functional connectivity compared to rSMG, to the left TPJ, precuneus, posterior cingulate cortex (PCC), and MPFC (see Figure 3.3 and Table 3.3). These results of different connectivity profiles for rSMG and rTPJ converge nicely with other parcellations of the temporo-parietal region (Bzdok et al., 2013; Mars et al., 2012). To investigate possible group differences in functional connectivity in the rSMG or the rTPJ network between ASD participants and healthy controls, we tested for an interaction between connectivity difference and group. Findings revealed significant differences in rTPJ ($FWE < .05$, Figure 3.4A) but not rSMG (Figure 3.4B) functional connectivity between the two groups (see also Table 3.3). Individuals with ASD displayed significantly reduced functional connectivity from rTPJ to lTPJ, precuneus, PCC, and MPFC. In addition a regression analysis within the rTPJ network using ADOS social interaction scores revealed that with increasing rTPJ-PCC coupling symptom severity decreased within the ASD sample (Figure 3.4C).

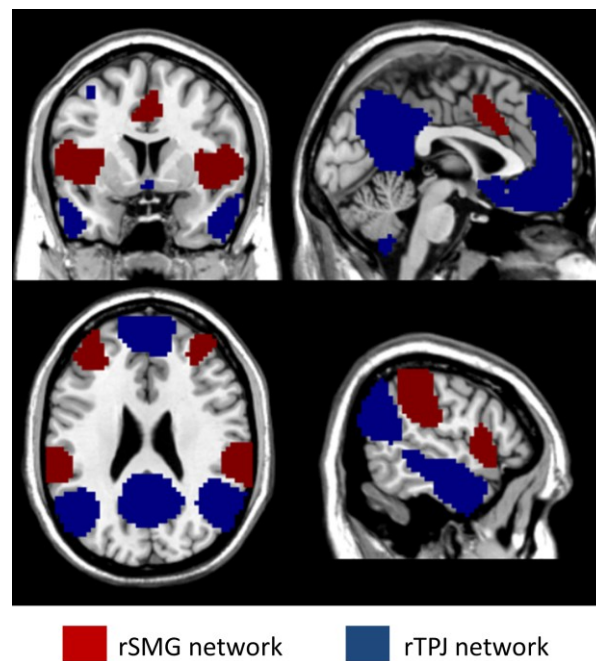


Figure 3.3. Display of the rSMG and the rTPJ network. Seed-based resting-state functional connectivity analysis revealed marked divergent connectivity profiles for rSMG and rTPJ (FWE < .05). RSMG shows greater functional coupling compared to rTPJ with lSMG, bilateral AI, IFG, DLPFC and MCC. Whereas rTPJ shows greater functional coupling compared to rSMG with lTPJ, MPFC, PCC, precuneus, temporal poles.

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Table 3.3. Peak coordinates from significant clusters observed in all analyses in study 2

Anatomical label	MNI coordinates			Cluster size	T-value
	x	y	z		
<i>rSMG > rTPJ</i>					
right SMG	63	-36	33	609	42.92
left SMG	-63	-39	36	426	16.87
right AI/IFG	48	12	0	869	10.34
left DLPFC	-42	45	30	326	9.95
left AI/IFG	-33	18	9	478	9.91
MCC	6	18	30	226	6.55
right Cingulate Gyrus	12	-27	42	14	5.74
left Superior Frontal Gyrus	-24	42	-15	2	4.57
<i>rTPJ > rSMG</i>					
right TPJ	51	-54	21	6125	39.54
left TPJ	-48	-60	24	1048	15.59
left Middle Temporal Gyrus	-60	-3	-21	1252	15.32
right Superior Frontal Gyrus	21	36	48	5226	14.91
left Cerebellum	-30	-78	-33	525	9.37
left Cerebellum	-6	-54	-45	184	9.09
right Cerebellum	30	-78	-33	430	8.57

left Middle Frontal Gyrus	-33	54	-6	2	4.72
<hr/>					
<i>HC > ASD > rSMG > rTPJ*</i>					
<hr/>					
					N.S.
<hr/>					
<i>HC > ASD > rTPJ > rSMG*</i>					
<hr/>					
left TPJ	-42	-66	21	311	3.61
left Middle Frontal Gyrus	-21	21	39	170	3.37
left Precuneus	-3	-63	27	611	3.29
right Superior Frontal Gyrus	6	66	0	236	3.15
right TPJ	39	-60	27	147	3.08
right Middle Frontal Gyrus	27	33	45	86	3.01
<hr/>					
<i>ADOS Social Interaction</i>					
<i>Regression in rTPJ network*</i>					
<hr/>					
left Middle Temporal Gyrus	-30	-66	21	211	4.31
right Posterior Cingulate	18	-54	18	167	4.28

*Results are cluster-wise corrected at FWE < .05.

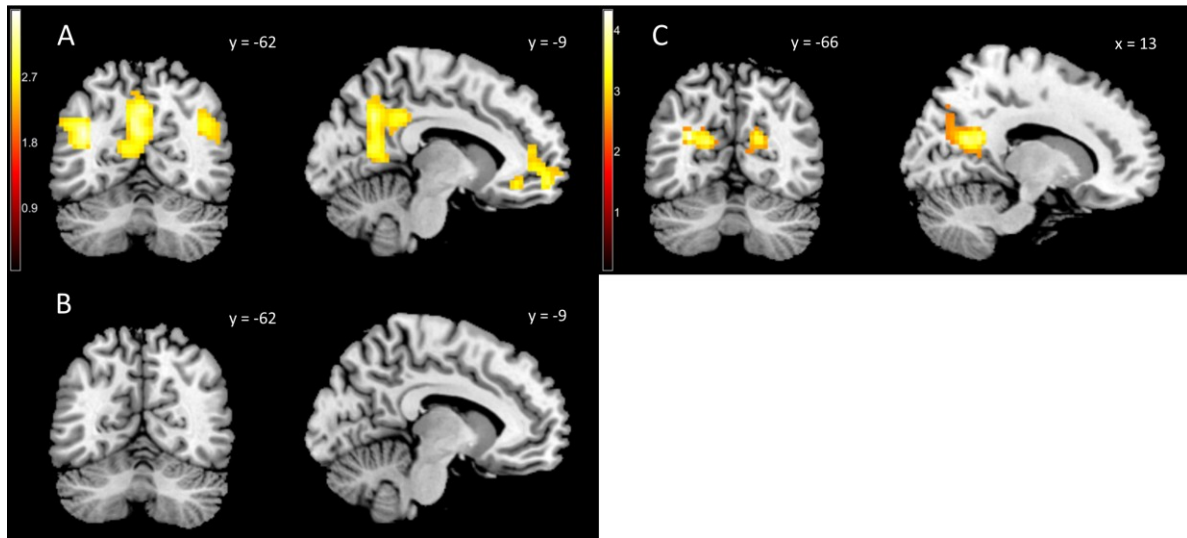


Figure 3.4. (A) Display of significant group difference in resting-state connectivity in the rTPJ network. Findings revealed significant differences in rTPJ but not rSMG functional connectivity between the two groups, with individuals with ASD showing reduced functional connectivity from rTPJ to ITPJ, precuneus, PCC and MPFC (FWE < .05, cluster corrected). (B) No significant group difference in resting-state connectivity in the rSMG network (FWE < .05, cluster corrected). (C) Brain regions showing increased coupling during rest with rTPJ with decreasing symptom severity (ADOS social interaction) within the ASD sample (FWE < .05, cluster corrected). Stronger connectivity between regions of the PCC with rTPJ in individuals with ASD predicts smaller ADOS social interaction scores.

Discussion

Previous studies have reported consistent findings on ToM deficits in ASD, however evidence for deficits in empathy in ASD has remained inconsistent, thus demanding a more detailed investigation. In the first study we focused on behaviourally investigating a more specific socio-affective ability, namely overcoming emotional egocentricity during empathic relating in individuals with ASD using the EEB Touch-paradigm (ETOP, Silani et al., 2013), while also assessing ToM abilities with an established task (Dziobek et al., 2006). In addition, Study

2 aimed to shed light on the integrity of neuronal networks associated with overcoming egocentricity (through self-other distinction) during empathy and ToM in ASD.

Study 1 found in line with the literature, that individuals with ASD show deficits in ToM (Baron-Cohen et al., 1985; Baron - Cohen, Wheelwright, Hill, Raste, & Plumb, 2001; Castelli et al., 2002; Dziobek et al., 2006; Happé, 1994; Klin, 2000). However, using the previously established ETOP, both, ASD participants and healthy controls, showed a significant EEB, comparable in size, suggesting no enhanced emotional egocentricity in ASD, and implicating relatively intact self-other distinction during empathic relating. Thus, according to these results, individuals with ASD are not more prone to project their own feelings onto others / bias their perception of feelings of others towards their own feelings than neurotypical individuals. Additionally, in ASD participants, ToM abilities were significantly related to symptom severity, while the EEB was not. These behavioural findings suggest that individuals with ASD might have specific deficits in ToM but not in self-other distinction during empathic relating, extending previous findings of intact empathy, that this is also the case even when emotional states between oneself and others are incongruent. The finding of an equally sized EEB in ASD as compared to healthy controls suggests that a more detailed account of social cognition deficits in ASD is required, in line with previous findings of spared socio-affective abilities (Bird et al., 2010; Hadjikhani et al., 2014; Jones et al., 2010; Lockwood et al., 2013; Rogers et al., 2007).

The analyses of Study 2 of networks underlying overcoming emotional egocentricity during empathy and ToM, showed that rSMG and rTPJ display highly specific resting-state connectivity profiles, further supporting the view of a functional segregation of these two networks (Silani et al., 2013). The rSMG, relative to rTPJ, was significantly connected to bilateral AI, MCC, i.e., regions which have been consistently shown to play a crucial role in emotion processing such as during interoception and empathy (Lamm et al., 2011; Singer et al., 2009; Singer et al., 2004). The rTPJ, relative to the rSMG, was in contrast predominantly

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connected with PCC, precuneus, MPFC, and ITPJ, all regions commonly associated with cognitive processes such as attentional processing, default mode brain function, as well as ToM. These differing resting-state profiles of rSMG and rTPJ are in accordance with similar parcellations of the temporo-parietal junction (Bzdok et al., 2013; Mars et al., 2012).

More importantly, the direct comparison of these networks between the healthy control and ASD samples revealed that in line with the behavioural patterns observed in Study 1, ASD participants displayed abnormal resting-state connectivity in the ToM network with significantly decreased functional connectivity of the rTPJ to the MPFC, PCC and ITPJ, but no significant functional connectivity decrease in the rSMG network. Additionally, symptom severity was shown to correlate negatively with increasing rTPJ/PCC coupling, speaking to the importance of the ToM network abnormalities in contributing to autistic symptomatology. These findings are in accordance with influential “disconnection theories” of ASD, suggesting that a disruption of a combination of frontotemporal, frontolimbic, frontoparietal and interhemispheric connections might be at the heart of the autistic condition (Belmonte et al., 2004; Courchesne & Pierce, 2005; Geschwind & Levitt, 2007; Just, Cherkassky, Keller, Kana, & Minshew, 2007; Just, Keller, Malave, Kana, & Varma, 2012). One problem of the “disconnection theories” of ASD is the lack of specificity, being short of explanation to why some abilities in ASD are deficient, some remain spared and some even seem to be enhanced (Geschwind & Levitt, 2007). Our results suggest that in the case of the temporo-parietal cortex in ASD, disrupted functional connectivity to other regions of the brain might be highly specific to TPJ but not the adjacent SMG, indicating that underconnectivity in ASD might just pertain to very specific brain networks. In sum, these resting-state connectivity findings complement our behavioural findings of unaffected emotional self-other distinction during empathy in ASD but deficient ToM. They suggest that intact functioning of the rSMG network links with intact self-other distinction during empathy in ASD, while aberrant

functioning of the rTPJ network possibly contributes to ToM deficits which in turn add to the autistic symptomatology.

Taken together, this study provides novel evidence that self-other distinction deficits and resulting egocentricity in ASD are mainly present in the cognitive domain, not extending into the affective domain of empathy. The finding of intact emotional self-other distinction is in accordance with some other findings showing partly intact empathic responding in ASD without comorbid alexithymia (Bird et al., 2010; Hadjikhani et al., 2014; Silani et al., 2008). Thus, importantly individuals with ASD exhibit even intact empathic relating, when self and other are in different emotional states, which represents another spared socio-affective ability in ASD. Together this study and previous ones point to the need to closely reconsider the exact features of the social deficits portrayed in ASD and to strive for a more fine-grained characterization of this developmental disorder. Identifying areas of intact functioning in ASD could help to inform targeted-intervention programs and in the case of spared socio-affective abilities could play a major role as compensatory mechanisms in therapy.

Limitations

It would have been favorable to perform the resting-state connectivity analyses on the behaviourally tested sample. Unfortunately however, as mentioned in the method section, resting-state scans were not available for the behavioural sample. On the upside the use of a large independent sample for the resting-state connectivity analyses, diminishes concerns about possible power issues for detecting effects.

In conclusion, this study demonstrated that while individuals with ASD exhibited known deficits in ToM, emotional egocentricity was comparable to that of healthy controls, suggesting intact self-other distinction during empathic relating. Importantly, via brain analyses we were able to associate self-other distinction during empathy on the one hand and ToM on the other to clearly divergent resting-state connectivity profiles with two adjacent seed regions in the right temporo-parietal junction, the rTPJ and rSMG, thus replicating

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previous findings. Importantly, and in line with the behavioural results, only the connectivity from rTPJ and not rSMG was significantly reduced for ASD patients compared to controls. This suggests that unlike ToM and its associated underlying rTPJ network, self-other distinction during empathy and its underlying rSMG network remain spared in individuals with ASD. These findings provide further detail for a more fine-grained characterization of social deficits in ASD, providing evidence for spared social-affective functioning, but deficiencies in socio-cognitive functioning.

References

- Aichhorn, M., Perner, J., Kronbichler, M., Staffen, W., & Ladurner, G. (2006). Do visual perspective tasks need theory of mind? *Neuroimage*, 30(3), 1059-1068.
- American Psychiatric Association. (2000). *Diagnostic and Statistical Manual of Mental Disorders, text revision* (4th ed., text rev.). Washington, DC : American Psychiatric Association.
- American Psychiatric Association. (2013). *Diagnostic and Statistical Manual of Mental Disorders* (5th ed.). Arlington,VA: American Psychiatric Association.
- Asperger, H. (1944). Die „Autistischen Psychopathen” im Kindesalter. *European Archives of Psychiatry and Clinical Neuroscience*, 117(1), 76-136.
- Baron-Cohen, S., Leslie, A. M., & Frith, U. (1985). Does the autistic child have a “theory of mind”? *Cognition*, 21(1), 37-46.
- Baron-Cohen, S., Wheelwright, S., Hill, J., Raste, Y., & Plumb, I. (2001). The “Reading the mind in the eyes” test revised version: A study with normal adults, and adults with asperger syndrome or high-functioning autism. *Journal of Child Psychology and Psychiatry*, 42(2), 241-251.
- Bastiaansen, J., Thioux, M., & Keysers, C. (2009). Evidence for mirror systems in emotions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1528), 2391-2404.
- Begeer, S., Bernstein, D. M., van Wijhe, J., Scheeren, A. M., & Koot, H. M. (2012). A continuous false belief task reveals egocentric biases in children and adolescents with Autism Spectrum Disorders. *Autism*, 16(4), 357-366.
- Belmonte, M. K., Allen, G., Beckel-Mitchener, A., Boulanger, L. M., Carper, R. A., & Webb, S. J. (2004). Autism and abnormal development of brain connectivity. *The Journal of Neuroscience*, 24(42), 9228-9231.

3. Manuscript of Study 2

- Birch, S. A., & Bloom, P. (2007). The curse of knowledge in reasoning about false beliefs. *Psychological Science, 18*(5), 382-386.
- Bird, G., & Cook, R. (2013). Mixed emotions: the contribution of alexithymia to the emotional symptoms of autism. *Translational Psychiatry, 3*(7). e285.
- Bird, G., Silani, G., Brindley, R., White, S., Frith, U., & Singer, T. (2010). Empathic brain responses in insula are modulated by levels of alexithymia but not autism. *Brain, 133*(5), 1515-1525.
- Brass, M., Ruby, P., & Spengler, S. (2009). Inhibition of imitative behaviour and social cognition. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*(1528), 2359-2367.
- Bzdok, D., Langner, R., Schilbach, L., Jakobs, O., Roski, C., Caspers, S., . . . Eickhoff, S. B. (2013). Characterization of the temporo-parietal junction by combining data-driven parcellation, complementary connectivity analyses, and functional decoding. *Neuroimage, 81*, 381-392.
- Castelli, F., Frith, C., Happé, F., & Frith, U. (2002). Autism, Asperger syndrome and brain mechanisms for the attribution of mental states to animated shapes. *Brain, 125*(8), 1839-1849.
- Courchesne, E., & Pierce, K. (2005). Why the frontal cortex in autism might be talking only to itself: local over-connectivity but long-distance disconnection. *Current Opinion in Neurobiology, 15*(2), 225-230.
- Dapretto, M., Davies, M. S., Pfeifer, J. H., Scott, A. A., Sigman, M., Bookheimer, S. Y., & Iacoboni, M. (2005). Understanding emotions in others: mirror neuron dysfunction in children with autism spectrum disorders. *Nature neuroscience, 9*(1), 28-30.
- Decety, J., & Lamm, C. (2007). The role of the right temporoparietal junction in social interaction: how low-level computational processes contribute to meta-cognition. *The Neuroscientist, 13*(6), 580-593.

- Dziobek, I., Fleck, S., Kalbe, E., Rogers, K., Hassenstab, J., Brand, M., . . . Convit, A. (2006). Introducing MASC: a movie for the assessment of social cognition. *Journal of autism and developmental disorders*, 36(5), 623-636.
- Frith, C. D., & Frith, U. (2012). Mechanisms of social cognition. *Annual review of psychology*, 63, 287-313.
- Gallese, V. (2001). The 'shared manifold' hypothesis. From mirror neurons to empathy. *Journal of consciousness studies*, 8(5-7), 33-50.
- Gallese, V. (2007). Before and below 'theory of mind': embodied simulation and the neural correlates of social cognition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1480), 659-669.
- Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends in cognitive sciences*, 2(12), 493-501.
- Geschwind, D. H., & Levitt, P. (2007). Autism spectrum disorders: developmental disconnection syndromes. *Current Opinion in Neurobiology*, 17(1), 103-111.
- Hadjikhani, N., Zürcher, N., Rogier, O., Hippolyte, L., Lemonnier, E., Ruest, T., . . . Billstedt, E. (2014). Emotional contagion for pain is intact in autism spectrum disorders. *Translational psychiatry*, 4(1), e343.
- Happé, F. G. (1994). An advanced test of theory of mind: Understanding of story characters' thoughts and feelings by able autistic, mentally handicapped, and normal children and adults. *Journal of Autism and Developmental Disorders*, 24(2), 129-154.
- Horn, W. (1962). Leistungsprüfsystem, LPS: Handanweisung für die Durchführung, Auswertung und Interpretation.
- Jones, A. P., Happé, F. G., Gilbert, F., Burnett, S., & Viding, E. (2010). Feeling, caring, knowing: different types of empathy deficit in boys with psychopathic tendencies and autism spectrum disorder. *Journal of Child Psychology and Psychiatry*, 51(11), 1188-1197.

3. Manuscript of Study 2

- Just, M. A., Cherkassky, V. L., Keller, T. A., Kana, R. K., & Minshew, N. J. (2007). Functional and anatomical cortical underconnectivity in autism: evidence from an fMRI study of an executive function task and corpus callosum morphometry. *Cerebral Cortex*, 17(4), 951-961.
- Just, M. A., Keller, T. A., Malave, V. L., Kana, R. K., & Varma, S. (2012). Autism as a neural systems disorder: a theory of frontal-posterior underconnectivity. *Neuroscience & Biobehavioral Reviews*, 36(4), 1292-1313.
- Klin, A. (2000). Attributing social meaning to ambiguous visual stimuli in higher-functioning autism and Asperger syndrome: the Social Attribution Task. *Journal of Child Psychology and Psychiatry*, 41(7), 831-846.
- Lamm, C., Decety, J., & Singer, T. (2011). Meta-analytic evidence for common and distinct neural networks associated with directly experienced pain and empathy for pain. *Neuroimage*, 54(3), 2492-2502.
- Lehrl, S., Triebig, G., & Fischer, B. (1995). Multiple choice vocabulary test MWT as a valid and short test to estimate premorbid intelligence. *Acta Neurologica Scandinavica*, 91(5), 335-345.
- Lockwood, P. L., Bird, G., Bridge, M., & Viding, E. (2013). Dissecting empathy: high levels of psychopathic and autistic traits are characterized by difficulties in different social information processing domains. *Frontiers in human neuroscience*, 7, 760.
- Lombardo, M. V., & Baron-Cohen, S. (2011). The role of the self in mindblindness in autism. *Consciousness and cognition*, 20(1), 130-140.
- Lord, C., Risi, S., Lambrecht, L., Cook, E. H., Leventhal, B. L., DiLavore, P. C., . . . Rutter, M. (2000). The Autism Diagnostic Observation Schedule-Generic: A standard measure of social and communication deficits associated with the spectrum of autism. *Journal of Autism and Developmental Disorders*, 30, 205-223.

- Lord, C., Rutter, M., & Le Couteur, A. (1994). Autism Diagnostic Interview-Revisited: a revised version of a diagnostic interview for caregivers of individuals with possible pervasive developmental disorders. *Journal of Autism and Developmental Disorders*, 24(5), 659-685.
- Mar, R. A. (2011). The neural bases of social cognition and story comprehension. *Annual review of psychology*, 62, 103-134.
- Mars, R. B., Sallet, J., Schuffelgen, U., Jbabdi, S., Toni, I., & Rushworth, M. F. (2012). Connectivity-based subdivisions of the human right "temporoparietal junction area": evidence for different areas participating in different cortical networks. *Cerebral Cortex*, 22(8), 1894-1903.
- Minio-Paluello, I., Baron-Cohen, S., Avenanti, A., Walsh, V., & Aglioti, S. M. (2009). Absence of embodied empathy during pain observation in Asperger syndrome. *Biological psychiatry*, 65(1), 55-62.
- Mitchell, J. P. (2009). Inferences about mental states. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1521), 1309-1316.
- Montag, C., Dziobek, I., Richter, I. S., Neuhaus, K., Lehmann, A., Sylla, R., . . . Gallinat, J. (2011). Different aspects of theory of mind in paranoid schizophrenia: evidence from a video-based assessment. *Psychiatry research*, 186(2), 203-209.
- Montag, C., Ehrlich, A., Neuhaus, K., Dziobek, I., Heekeren, H. R., Heinz, A., & Gallinat, J. (2010). Theory of mind impairments in euthymic bipolar patients. *Journal of Affective Disorders*, 123(1), 264-269.
- Nickerson, R. S. (2001). The projective way of knowing: A useful heuristic that sometimes misleads. *Current Directions in Psychological Science*, 10(5), 168-172.
- Premack, D., & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *Behavioral and brain sciences*, 1(04), 515-526.

3. Manuscript of Study 2

- Pronin, E. (2008). How we see ourselves and how we see others. *Science*, 320(5880), 1177-1180.
- Ramsey, R., Hansen, P., Apperly, I., & Samson, D. (2013). Seeing it my way or your way: Frontoparietal brain areas sustain viewpoint-independent perspective selection processes. *Journal of cognitive neuroscience*, 25(5), 670-684.
- Ritter, K., Dziobek, I., Preißler, S., Rüter, A., Vater, A., Fydrich, T., . . . Roepke, S. (2011). Lack of empathy in patients with narcissistic personality disorder. *Psychiatry research*, 187(1), 241-247.
- Rogers, K., Dziobek, I., Hassenstab, J., Wolf, O. T., & Convit, A. (2007). Who cares? Revisiting empathy in Asperger syndrome. *Journal of Autism and Developmental Disorders*, 37(4), 709-715.
- Royzman, E. B., Cassidy, K. W., & Baron, J. (2003). " I know, you know": Epistemic egocentrism in children and adults. *Review of General Psychology*, 7(1), 38-65.
- Santiesteban, I., Banissy, M. J., Catmur, C., & Bird, G. (2012). Enhancing social ability by stimulating right temporoparietal junction. *Current Biology*, 22(23), 2274-2277.
- Santiesteban, I., White, S., Cook, J., Gilbert, S. J., Heyes, C., & Bird, G. (2012). Training social cognition: from imitation to theory of mind. *Cognition*, 122(2), 228-235.
- Satterthwaite, T. D., Elliott, M. A., Gerraty, R. T., Ruparel, K., Loughead, J., Calkins, M. E., . . . Gur, R. E. (2013). An improved framework for confound regression and filtering for control of motion artifact in the preprocessing of resting-state functional connectivity data. *Neuroimage*, 64, 240-256.
- Senju, A., Southgate, V., Miura, Y., Matsui, T., Hasegawa, T., Tojo, Y., . . . Csibra, G. (2010). Absence of spontaneous action anticipation by false belief attribution in children with autism spectrum disorder. *Development and psychopathology*, 22(02), 353-360.

- Senju, A., Southgate, V., White, S., & Frith, U. (2009). Mindblind eyes: an absence of spontaneous theory of mind in Asperger syndrome. *Science*, 325(5942), 883-885.
- Silani, G., Bird, G., Brindley, R., Singer, T., Frith, C., & Frith, U. (2008). Levels of emotional awareness and autism: an fMRI study. *Social Neuroscience*, 3(2), 97-112.
- Silani, G., Lamm, C., Ruff, C. C., & Singer, T. (2013). Right Supramarginal Gyrus Is Crucial to Overcome Emotional Egocentricity Bias in Social Judgments. *The Journal of Neuroscience*, 33(39), 15466-15476.
- Singer, T. (2012). The past, present and future of social neuroscience: A European perspective. *Neuroimage*, 61(2), 437-449.
- Singer, T., Critchley, H. D., & Preuschoff, K. (2009). A common role of insula in feelings, empathy and uncertainty. *Trends in cognitive sciences*, 13(8), 334-340.
- Singer, T., & Lamm, C. (2009). The social neuroscience of empathy. *Annals of the New York Academy of Sciences*, 1156(1), 81-96.
- Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R. J., & Frith, C. D. (2004). Empathy for pain involves the affective but not sensory components of pain. *Science*, 303(5661), 1157-1162.
- Sommer, M., Döhl, K., Sodian, B., Meinhardt, J., Thoermer, C., & Hajak, G. (2007). Neural correlates of true and false belief reasoning. *Neuroimage*, 35(3), 1378-1384.
- Song, X. W., Dong, Z. Y., Long, X. Y., Li, S. F., Zuo, X. N., Zhu, C. Z., . . . Zang, Y. F. (2011). REST: A Toolkit for Resting-State Functional Magnetic Resonance Imaging Data Processing. *PLOS ONE*, 6(9).
- Spengler, S., von Cramon, D. Y., & Brass, M. (2009). Control of shared representations relies on key processes involved in mental state attribution. *Human brain mapping*, 30(11), 3704-3718.

3. Manuscript of Study 2

- Spengler, S., von Cramon, D. Y., & Brass, M. (2010). Resisting motor mimicry: control of imitation involves processes central to social cognition in patients with frontal and temporo-parietal lesions. *Social Neuroscience*, 5(4), 401-416.
- Steinbeis, N., Bernhardt, B. C., & Singer, T. (2014). Age-related differences in function and structure of rSMG and reduced functional connectivity with DLPFC explains heightened emotional egocentricity bias in childhood. *Social Cognitive and Affective Neuroscience*, nsu057.
- Taylor, G. J., Ryan, D., & Bagby, R. M. (1985). Toward the development of a new self-report alexithymia scale. *Psychotherapy and Psychosomatics*, 44(4), 191-199.
- Van Boven, L., & Loewenstein, G. (2003). Social projection of transient drive states. *Personality and Social Psychology Bulletin*, 29(9), 1159-1168.

**Preserved self-other distinction during empathy in autism is linked to network integrity
of right supramarginal gyrus**

Supplemental Information

Imaging Sample

The Autism Brain Imaging Data Exchange (ABIDE) database, provides structural and functional MRI data together with clinical and demographic information from individuals with ASD and healthy controls (Di Martino et al., 2013). ASD diagnosis was based on expert clinical opinion and the Autism Diagnostic Observation Schedule, ADOS (Lord et al., 2000), and/or the Autism Diagnostic Interview-Revised, ADI-R (Lord et al., 1994). More detailed information about the ABIDE consortium and site-specific details are available at http://fcon_1000.projects.nitric.org/indi/abide.

The sample selected for this study consisted of male participants from 7 different sites: 1) California Institute of Technology (n = 26, 13 ASDs, 13 healthy controls); 2) University of Leuven (n = 27, 13 ASDs, 14 healthy controls); 3) Olin, Institute of Living at Hartford Hospital (n = 10, 5 ASDs, 5 healthy controls); 4) University of Pittsburgh, School of Medicine (n = 21, 10 ASDs, 11 healthy controls); 5) Trinity Centre for Health Sciences (n = 19, 9 ASDs, 10 healthy controls); 6) University of Utah, School of Medicine (n = 5, 5 healthy controls) and 7) University of Michigan (n = 55, 34 ASDs, 21 healthy controls).

EEB Touch-Paradigm (ETOP)

Before the start, two participants unknown to each other were familiarized with the rating scale and performed 6 practice trials for each experimental condition. Participants started with the individual conditions which were blocked and counterbalanced. In the

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individual self condition a picture (size 336 X 336 pixels) appeared on the touch screen (800 x 600 pixels resolution, 15 inch screen, viewing distance ~ 40 cm) accompanied by a corresponding tactile stimulation of the participant's left hand at 1 Hz for 3000 ms. hidden behind a curtain preventing them to observe the different stimulation materials. In the individual other condition, the trial structure remained the same, but the participant did not receive any tactile stimulation. Instead, he was instructed to judge the pleasantness of the tactile experience for the other participant based on the picture indicating what tactile stimulation the other participant received. Each run consisted of 30 pseudo-randomized trials, with 10 pleasant, 10 neutral and 10 unpleasant visuo-tactile stimuli. This resulted in a three-factorial mixed design with the two within-subjects factors *target* (self, other judgment) and *valence* (pleasant, neutral and unpleasant stimulation) and the between-subjects factor *group* (healthy controls and ASD).

In the following simultaneous conditions both participants in the room received tactile stimulation simultaneously and were instructed to either judge the pleasantness of their own tactile experience (simultaneous self condition) or judge the pleasantness of the tactile experience for the other person (simultaneous other condition). In these conditions two pictures appeared on the screen, while the left picture with the label "Self" corresponded to the tactile stimulation the participant received, the right picture with the label "Other" corresponded to the touch the other person received. The touch experiences of the two participants could be either affectively congruent or incongruent. The simultaneous conditions were blocked and counterbalanced. The EEB was defined as the difference between ratings in incongruent and congruent trials when judging the other, as compared to the difference when judging one's own feelings. In this way, the simultaneous self condition served to control for general perceptual or cognitive confounds- such as visual and affective stimulus comparison, detection of incongruency, or overcoming general response conflict. For the simultaneous conditions each run consisted of 40 pseudo-randomized trials, with 20 pleasant (10

congruent/10 incongruent) and 20 unpleasant (10 congruent/10 incongruent) visuo-tactile stimuli.. This resulted in a four-factorial mixed design with the three within-subjects factors *target* (self, other judgment), *valence* (pleasant, unpleasant stimulation), and *congruence* (congruent, incongruent stimulation of participant and other) and the between-subjects factor *group* (healthy controls and ASD). The significant triple interaction of *target X congruency X group* would be indicative of a significant group difference in the size of the EEB. Data analysis was performed using the IBM SPSS statistics software, version 19.0.

Resting-state connectivity analysis

Data were processed using the data processing assistant for the resting-state fMRI toolbox (DPARF, Song et al., 2011) for Matlab. The toolbox is based on the Statistical Parametric Mapping toolbox (SPM8, <http://www.fil.ion.ucl.ac.uk/spm>). In brief, preprocessing discarded the first 10 volumes, performed slice time correction, motion correction and realignment, and co-registered the functional time series to the corresponding T1-weighted MRI. Images underwent DARTEL-based segmentation and registration, followed by nuisance covariate regression to remove effects of average WM and CSF signal, as well as 6 motion parameters (3 translations and 3 rotations). To deal more thoroughly with possible differential motion artifacts in our samples we included the scrubbing approach advocated by Power, Barnes, Snyder, Schlaggar, and Petersen (2012), which models bad time points (based on the framewise displacement threshold, FD (Power), of 0.5mm or higher; together with one time point before and one time point after each such time point] as separate regressors during the nuisance covariate correction. Time series were band-pass filtered to be within the 0.01 and 0.08 Hz band (Satterthwaite et al., 2013), normalized to MNI space, resampled to 3mm voxels, and spatially smoothed using a 8 mm Full-Width-at-Half-Maximum (FWHM) isotropic Gaussian kernel. The rSMG region was based on the overlap of activations from two separate fMRI experiments using the ETOP, which independently

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confirmed the crucial involvement of rSMG in overcoming the EEB (Silani et al., 2013). The rSMG region emerged after the contrast (Other Judgment: Incongruent > Congruent) > (Self Judgment: Incongruent > Congruent). The rTPJ region was based on meta-analytic activation of rTPJ in story-based and nonstory based ToM studies, collected in a coordinate-based meta-analysis by Mar (2011). Functional connectivity was calculated as the time series correlation between the mean time series of the seed region and the time series of all brain voxels. Time-series correlation coefficients underwent a Fisher r-to-z transformation to render the data more normally distributed.

Results (Individual conditions)

Investigating whether the emotion induction worked for both groups the individual conditions were analysed with an analysis of variance (ANOVA) on the affective ratings with target (self vs. other) and valence (positive, neutral, negative) as within-subjects factors and group (ASD vs. healthy controls) as between-subjects factor.

The results revealed a significant main effect of valence ($F_{1,96} = 221.48, P < .001, \eta_p^2 = .822$), and target ($F_{1,48} = 8.33, P < .001, \eta_p^2 = .148$), as well as a significant target by valence ($F_{1,96} = 13.09, P < .001, \eta_p^2 = .214$) and valence by group interaction ($F_{1,96} = 6.40, p < .001, \eta_p^2 = .118$). There was no significant main effect of group or further significant interaction with group ($F_s < 1.84, P_s > .164$). Post-hoc tests showed that the ASD group rated the negative and positive emotions less intense for self and other. After controlling for alexithymia, no group differences remained, indicating equally effective emotion induction for both groups by means of visuo-tactile stimulation.

Supplemental References

- Di Martino, A., Yan, C. G., Li, Q., Denio, E., Castellanos, F. X., Alaerts, K., . . . Milham, M. P. (2013). The autism brain imaging data exchange: towards a large-scale evaluation of the intrinsic brain architecture in autism. *Molecular Psychiatry*, *19*, 659-667.
- Lord, C., Risi, S., Lambrecht, L., Cook, E. H., Leventhal, B. L., DiLavore, P. C., . . . Rutter, M. (2000). The Autism Diagnostic Observation Schedule-Generic: A standard measure of social and communication deficits associated with the spectrum of autism. *Journal of Autism and Developmental Disorders*, *30*, 205-223.
- Lord, C., Rutter, M., & Le Couteur, A. (1994). Autism Diagnostic Interview-Revisited: a revised version of a diagnostic interview for caregivers of individuals with possible pervasive developmental disorders. *Journal of Autism and Developmental Disorders*, *24*(5), 659-685.
- Mar, R. A. (2011). The neural bases of social cognition and story comprehension. *Annual review of psychology*, *62*, 103-134.
- Power, J. D., Barnes, K. A., Snyder, A. Z., Schlaggar, B. L., & Petersen, S. E. (2012). Spurious but systematic correlations in functional connectivity MRI networks arise from subject motion. *Neuroimage*, *59*(3), 2142-2154.
- Satterthwaite, T. D., Elliott, M. A., Gerraty, R. T., Ruparel, K., Loughhead, J., Calkins, M. E., . . . Gur, R. E. (2013). An improved framework for confound regression and filtering for control of motion artifact in the preprocessing of resting-state functional connectivity data. *Neuroimage*, *64*, 240-256.
- Silani, G., Lamm, C., Ruff, C. C., & Singer, T. (2013). Right Supramarginal Gyrus Is Crucial to Overcome Emotional Egocentricity Bias in Social Judgments. *The Journal of Neuroscience*, *33*(39), 15466-15476.

3. Manuscript of Study 2

Song, X. W., Dong, Z. Y., Long, X. Y., Li, S. F., Zuo, X. N., Zhu, C. Z., . . . Zang, Y. F. (2011). REST: A Toolkit for Resting-State Functional Magnetic Resonance Imaging Data Processing. *PLOS ONE*, 6(9).

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Empathy in depression: Egocentric and altercentric biases and the role of alexithymia

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Abstract

Background. Major depressive disorder (MDD) has been associated with deficits in empathy, however the exact nature of these deficits and their relation to concurrent alexithymia has remained elusive. In this study we tested under which conditions MDD patients show deficient empathy, investigating empathic relating during congruent and incongruent emotional perspectives of self and other in MDD patients with high and low alexithymia.

Method. Healthy controls and currently depressed MDD patients with low ($n = 28$, $n = 11$) or high ($n = 14$, $n = 18$) alexithymia performed an emotional egocentricity paradigm inducing emotions by means of tactile stimulation. This task allowed to measure empathy during a simple condition, when simulation suffices, and a complex condition, when emotional perspectives of self and other differ.

Results. Only alexithymia but not depression decreased empathy in the simple empathy condition. However, when emotional perspectives of self and other differ, MDD patients showed an egocentric bias during empathic judgments and an altercentric bias during emotional self judgments (suggesting heightened emotional contagion), both independent of alexithymia. Across the entire sample, alexithymia decreased the size of the egocentric bias during empathic judgments.

Conclusions. These results suggest that MDD patients show intact empathic judgments, when simple simulation is not hampered by concurrent alexithymia. In more complex situations when simulation alone does not suffice and incongruent emotional perspectives of self and other have to be resolved, MDD patients are prone to egocentric and altercentric biases.

Introduction

Depression is often characterized by deficits in social functioning (Hirschfeld et al., 2000). Empathy, the ability to understand and share feelings of others represents an important cornerstone of social cognition as the affective route to understanding others (Singer, 2012; Singer et al., 2004). Findings of empathic deficits in depression have been mixed so far (Thoma et al., 2011; Wilbertz et al., 2010; Wolkenstein et al., 2011), with the greatest consensus on heightened empathic distress (Schreiter & Pijnenborg, 2013). This lack of clear evidence for empathy deficits in depression may be related to two important reasons. First, the emotional states of self and other during empathy tasks have never been varied, which however, as we will argue later, is particularly relevant to more complex everyday empathic relating. Secondly, and very importantly alexithymia, a common comorbid personality trait in depression (Honkalampi et al., 2000; Taylor & Bagby, 2004), associated with deficits in empathy and emotional awareness (Bird et al., 2010; Moriguchi et al., 2007; Silani et al., 2008), has commonly not been accounted for. Thus, in this study we aimed to address these issues to arrive at a more comprehensive picture of empathic relating in depression.

Generally human interpersonal understanding often relies on mechanisms of self simulation, as for example in the case of empathy, where one's own feeling states tend to be used to simulate the feeling state of another (Bastiaansen et al., 2009; Brass et al., 2009; Decety & Lamm, 2007; Gallese, 2001, 2007; Gallese & Goldman, 1998; Mitchell, 2009; Nickerson, 2001; Silani et al., 2013; Singer, 2012; Singer et al., 2004; Van Boven & Loewenstein, 2003). However such simulation mechanisms fail in making sense of other's mental states in situations where mental states of self and other clearly differ. For instance it would be erroneous to assume that someone was happy just because we ourselves feel happy, when he is clearly sad. Thus, one important aspect when considering empathic relating is the congruency of the emotional perspectives of self and other. In everyday situations, empathic relating becomes much more complex, as emotional perspective of self and other are not

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always perfectly aligned but are instead often very different. In these cases, simple simulation mechanisms fail and resulting egocentric biases need to be overcome to arrive at accurate empathic judgments. A recent study demonstrated, that healthy adults do show an egocentric bias during empathic relating, while functioning of the right supramarginal gyrus (rSMG) was involved in overcoming such emotional egocentricity. In addition two developmental studies provided evidence for increased emotional egocentricity during empathic relating in children relative to adults, which was associated with deficits in emotional conflict processing and reduced functional coupling of dorsolateral prefrontal cortex (DLPFC) with rSMG (Hoffmann, Singer, & Steinbeis, in press; Steinbeis et al., 2014).

Evidence of increased egocentric bias during empathic relating in depression is however sparse and comes mostly from clinical reports and anecdotal evidence, an experimental investigation is yet missing. Findings of deficient emotion regulation abilities (Berpohl et al., 2009; Joormann & Gotlib, 2010; Kanske et al., 2012), heightened processing of negative stimuli (Leppänen, 2006; Sterzer et al., 2011) and deficient emotional and non-emotional emotional conflict processing (Etkin & Schatzberg, 2011; Kanske & Kotz, 2012; F. Murphy et al., 1999; Paelecke-Habermann et al., 2005; Waring et al., 2013) could suggest that individuals with depression, even if they possess intact simulation under simple empathy conditions, might show difficulties and egocentric bias under more complex empathy conditions, when needing to detach from their own emotional perspective to take the incongruent emotional perspective of another person.

While empathic judgments of another persons' emotional perspective can be influenced by an egocentric bias, emotional judgments of one's own emotional perspective can also be influenced by another persons' emotional perspective, leading to an altercentric bias. Such an altercentric bias during emotional self judgments, represents a form of emotional contagion, the automatic and implicit tendency to resonate and be affected by another person's emotional perspective (Singer & Lamm, 2009). To investigate the

altercentric bias during empathic self judgments in depression, is of interest as for example heightened personal distress is commonly reported in depression (Schreiter & Pijnenborg, 2013). Personal distress represents a self-oriented, aversive emotional reaction, such as anxiety or discomfort, towards another person's emotional state (Davis, 1980), thus possibly suggesting that individuals with depression have difficulties detaching emotional perspectives of others from their own, showing heightened emotional contagion.

Whether under simple or more complex empathy conditions, alexithymia, a common comorbid personality trait in recurrent depressive disorder (Honkalampi et al., 2000; Taylor & Bagby, 2004), needs to be accounted for as it has been associated with deficits in empathy and emotional awareness (Bird et al., 2010; Moriguchi et al., 2007; Silani et al., 2008). Alexithymia is characterized by difficulties in identifying and describing one's own emotional perspective (Sifneos, 1973), and has been shown to be normally distributed in the general population (Franz et al., 2008). Deficits in empathy and emotional awareness in depression might thus be dependent on concurrent alexithymia, rather than the diagnosis of depression itself. Initial evidence from autism spectrum disorder (ASD) suggests that some deficits in empathy in ASD can be explained by comorbid alexithymia (Bird & Cook, 2013). Alexithymia is linked among other brain regions to functioning of the anterior insula, which represents an important node of the rSMG network (Bird et al., 2010; Silani et al., 2013; Steinbeis et al., 2014). It therefore seems crucial to further elucidate the role of alexithymia in relation to empathic relating, under simple conditions, when emotional perspectives of self and other do not differ and under complex conditions, when emotional perspectives of self and other do differ. As the findings above suggest, alexithymia affects empathic simulation during simple conditions in healthy controls and in ASD and most likely also in depression. How alexithymia affects empathic relating under complex conditions in healthy controls as well as in depression remains unknown. It could be suggested that individuals with alexithymia would experience diminished emotional conflict due to diminished emotional

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awareness, finding it easier to detach from their own emotional perspective during empathic relating, leading to a decreased egocentric bias. Emotional contagion on the other hand, being a largely unconscious process, might be less affected by alexithymia thus, levels of emotional awareness.

In this study we used the established Emotional Egocentricity Bias (EEB) Touch-Paradigm (ETOP, Silani et al., 2013), which allows to measure empathic relating under simple and complex conditions, varying the emotional perspectives of self and other. Thus the first aim of this study was to investigate empathic relating in depressed patients and healthy controls under simple conditions, when simple simulation mechanisms suffice to arrive at an accurate empathic judgment. The second aim was to investigate empathic relating in depressed patients and healthy controls under complex conditions, when emotional perspectives of self and other differ, and egocentric bias during empathic judgments and altercentric bias, i.e. heightened emotional contagion during emotional self judgments, can emerge. It has to be noted that in some previous studies on egocentric bias during empathic relating in healthy adults and children (Hoffmann et al., in press; Silani et al., 2013) the altercentric interference has been minimal and subtracted from the egocentric bias. Since the altercentric bias as a form of emotional contagion is of interest on its own in the present study, we analyze the two types of bias separately. The third aim was to investigate the role of alexithymia on empathic relating under both simple and complex conditions. We therefore tested depressed patients and healthy controls with high and low alexithymia.

In sum we hypothesized first, that if simulation processes are intact in depression, depressed patients might show normal empathic relating under simple conditions, when alexithymia is controlled for. Secondly we expected individuals with depression to have particular problems in resolving conflicting emotional perspectives, thus suggesting increased egocentric and altercentric biases relative to healthy controls, during empathic relating under complex conditions. Connected to this hypothesis, we expected both biases to be greater in

depression, when negative perspectives have to be detached from, considering that depression has been associated with heightened processing of negative stimuli. Third, alexithymia was hypothesized to influence the size of the egocentric bias during empathic relating, as less emotional awareness should decrease the emotional conflict between the different perspectives. Fourth, we expected, that alexithymia would have less of an influence on the altercentric bias, as emotional contagion should not be affected that much by emotional awareness.

Methods

Participants

29 patients with depression were recruited through the inpatient clinic of the Charité-Universitätsmedizin Berlin, or were referred to us by specialized clinicians. 42 healthy control (HC) participants matched to the patients in terms of years of education, age and gender with no history of psychiatric or neurological disorders were recruited by public notices and from project databases of the Charité-Universitätsmedizin Berlin and the Freie Universität Berlin. Participants were assessed for psychiatric disorders using a structured clinical interview (SCID-I; Wittchen, Wunderlich, Gruschwitz, & Zaudig, 1997). Diagnosis of acute state of depression as according to DSM-IV was confirmed with no other primary diagnoses using the SCID-I. All participants completed the Beck Depression Inventory (BDI, Hautzinger, Bailer, Worall, & Keller, 1995), and were also assessed with the Hamilton Depression Rating Scale (HAM-D-17, M. Hamilton, 1960). Additionally, participants completed the Toronto alexithymia scale (Bagby, Parker, & Taylor, 1994), and a measure of crystallized intelligence (Wortschatztest, WST, a vocabulary test part of the HAWIE-R, the German adaptation of the Wechsler Adult Intelligence Scale, Schmidt & Metzler, 1992) (see Table 1). All MDD patients were medicated. There were significant group differences in terms of age and

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crystalline IQ. Healthy participants had a higher mean age, while the crystalline IQ was slightly lower for the MDD group compared to the healthy controls. Therefore, age and crystalline IQ were used as covariates in all analyses.

Low and high alexithymia was defined based on a large representative German population sample (Franz et al., 2008). The 66th percentile equaling the TAS -20 sum core of 53 for men and 52 for women was used as a cut-off to represent high alexithymia. We used this cut-off to distinguish between individuals with high alexithymia (equal to and above 53/52) and those with low alexithymia (below 53/52).

Table 4.1. Demographic and clinical characteristics of the participants

	Healthy Controls		MDD patients		Significant effects ($p < 0.05$)
	<i>Low alexithymia</i>	<i>High alexithymia</i>	<i>Low alexithymia</i>	<i>High alexithymia</i>	
Sample size	28	14	11	18	
Gender	9 males	8 males	2 males	8 males	
Age	42.2 (13.0)	61.5 (18.5)	47.5 (12.7)	39.4 (11.7)	d
Education	15.8 (2.9)	18.7(8.0)	16.4 (3.9)	14.3 (2.9)	d * a
Verbal IQ (WST)	105.3 (8.2)	111.6 (10.7)	98.3 (14.4)	100.7 (5.4)	d
BDI	2.0 (3.3)	7.8 (7.5)	26.9 (8.9)	35.2 (10.9)	d, a
HAMD-21	0.70 (1.6)	1.4 (2.9)	19.0 (2.2)	21.3 (3.8)	d, a
TAS-20	38.3 (7.5)	60.3 (6.3)	44.0 (4.6)	61.0 (6.6)	a

d = significant depression group main effect; a = significant alexithymia group main effect; d * a = significant depression group by alexithymia group interaction.

EEB Touch-Paradigm (ETOP)

The design and procedure of this paradigm was identical to that reported in Silani et al. (2013). Participants unknown to each other were assigned pairwise to an experimental session. Sitting back to back in front of a touch screen (800 x 600 pixels resolution, 15 inch screen, viewing distance ~40 cm) they were asked to rate the pleasantness or unpleasantness of the tactile stimulation of their left palm hidden behind a curtain preventing them to observe the different stimulation materials. Before the start, participants were familiarized with the rating scale and performed 6 practice trials for each experimental condition. Participants started with the simple conditions instructed to either judge the pleasantness of their own touch stimulation (individual self condition) or the pleasantness of the tactile stimulation for the other person (individual other condition). The simple conditions were blocked and counterbalanced. In the individual self condition a picture appeared on the screen accompanied by a corresponding tactile stimulation of the participant's left hand at 1 Hz for 3000 ms (e.g. a picture of a rose while the participant was touched by a silky object). Immediately after the stimulation phase participants judged the pleasantness or unpleasantness of the tactile experience by using a rating scale (ranging from -10 to 10) on the touch screen, within 3000 ms response time. In the individual other condition, the trial structure was the same, but the participant did not receive any tactile stimulation. Instead, he was instructed to judge the pleasantness of the tactile experience for the other participant based on the picture indicating what tactile stimulation the other participant received. Each run consisted of 30 pseudo-randomized trials, with 10 pleasant, 10 neutral and 10 unpleasant visuo-tactile stimuli. This resulted in a four-factorial mixed design with the two within-subjects factors *target* (self, other judgment) and *valence* (pleasant, neutral and unpleasant stimulation) and the between-subjects factors *depression group* (healthy controls and MDD patients) and *alexithymia group* (high alexithymia and low alexithymia).

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In the following complex conditions both participants in the room received tactile stimulation simultaneously, and were instructed to either judge the pleasantness of their own tactile experience (simultaneous self condition) or judge the pleasantness of the tactile experience for the other person (simultaneous other condition). The complex conditions were blocked and counterbalanced. In these conditions two pictures appeared on the screen, while the left picture with the label “Self” on top corresponded to the tactile stimulation that the participant received, the right picture with the label “Other” corresponded to the touch that the other person received. The touch experiences of the two participants could be either affectively congruent (e.g. both touched by pleasant materials, e.g. silk and fur) or incongruent (e.g. one gets touched by a pleasant, the other by an unpleasant material, e.g. silk and rubber spider). The EEB was defined as the difference between ratings in incongruent and congruent trials when judging the other, as compared to the difference when judging one’s own emotion. For the complex conditions each run consisted of 40 pseudo-randomized trials, with 20 pleasant (10 congruent/10 incongruent) and 20 unpleasant (10 congruent/10 incongruent) visuo-tactile stimuli. This resulted in a four-factorial mixed design with the three within-subjects factors *target* (self, other judgment), *valence* (pleasant, unpleasant stimulation), and *congruence* (congruent, incongruent stimulation of participant and other) and the between-subjects factor *group* (healthy controls and MDD patients) and *alexithymia group* (high alexithymia and low alexithymia). Data analysis was performed using the IBM SPSS statistics software, version 19.0.

Inhibitory control

Inhibitory control was assessed with a Go/NoGo task, to control for differences in executive functions. In this task a blue square represented a Go stimulus and a red square a NoGo stimulus (intertrial intervals randomly 950 ms or 1500 ms). 90 Go trials and 60 NoGo trials were randomly presented. Participants had to respond quickly with a button-press to the

presentation of the Go stimuli, while withholding a response to the presentation of the NoGo stimuli. Response inhibition was measured by the ability to inhibit successfully the response to NoGo stimuli. A d-prime score was calculated as measure of response sensitivity ($d' = Z(\text{hit rate}) - Z(\text{false alarm rate})$).

Empathy trait measure

Trait empathy was assessed with the Interpersonal Reactivity Index (IRI; Davis, 1980), differentiating empathy into 4 components (empathic concern, personal distress, perspective-taking, fantasy).

Results

EEB Touch-Paradigm (ETOP)

Simple conditions. Investigating whether empathic simulation is intact in depression, the simple conditions were analysed with an analysis of covariance (ANCOVA) on the affective ratings with target (self vs. other) and valence (positive, neutral, negative) as within-subjects factors and depression group (depressed patients vs. healthy controls) and alexithymia group (high alexithymia vs. low alexithymia) as between-subjects factors and age, education, and crystalline IQ as covariates.

The results revealed a significant main effect of valence ($F_{2, 128} = 115.411, p < .001, \eta_p^2 = .194$), and a marginally significant main effect of alexithymia group ($F_{1, 64} = 3.441, p = .068, \eta_p^2 = .051$). There were no further significant main effects or interactions ($F_s < 1.990, p_s > .141$). The data indicates that empathic simulation as well as emotional interoception are intact in depression, and only decreased by alexithymia (see Figure 4.1a).

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Complex conditions. In previous studies simultaneous other and self ratings have been included in a single model, to investigate for a stronger egocentric effect against the altercentric effect. Because of our interest in both the egocentric and altercentric effects, we mainly analysed them separately, but used the previous model first to replicate previous findings. An ANCOVA on the affective ratings with target (self, other), congruency (congruent, incongruent), and valence (positive, negative) as within-subjects factors and depression group and alexithymia group as between-subjects factors, as well as age, education, and crystalline IQ as covariates was performed. There was a significant target by congruency by alexithymia group interaction ($F_{1, 64} = 5.946, p = 0.018, \eta_p^2 = 0.085$), but no significant target by congruency by depression group interaction ($F_{1, 64} = 1.094, p = 0.300, \eta_p^2 = 0.017$), suggesting that the extent of egocentric bias against the altercentric bias was not modulated by depression, but by alexithymia. This suggests that the emotional egocentricity as measured with the typical EEB, decreased with alexithymia.

To look specifically at an egocentric bias during empathic relating, not subtracting the altercentric bias, we analysed the simultaneous other ratings separately. There was a significant main effect of congruency ($F_{1, 64} = 4.281, p = 0.043, \eta_p^2 = 0.063$). Importantly there was a marginally significant congruency by depression group interaction ($F_{1, 64} = 3.379, p = 0.071, \eta_p^2 = 0.050$), and a significant congruency by alexithymia group interaction ($F_{1, 64} = 5.560, p = 0.021, \eta_p^2 = 0.080$), as well as a significant congruency by emotion by depression group interaction ($F_{1, 64} = 7.817, p = 0.007, \eta_p^2 = 0.109$). Response inhibition as measured with the d-prime score, did not account for the increased egocentric bias in depression ($F_{1, 64} = 3.379, p = 0.071, \eta_p^2 = 0.050$). These results do indeed suggest increased egocentric bias during empathic relating under complex conditions for depressed patients compared to healthy controls, while high alexithymia significantly decreased the egocentric bias (see Figure 4.1b).

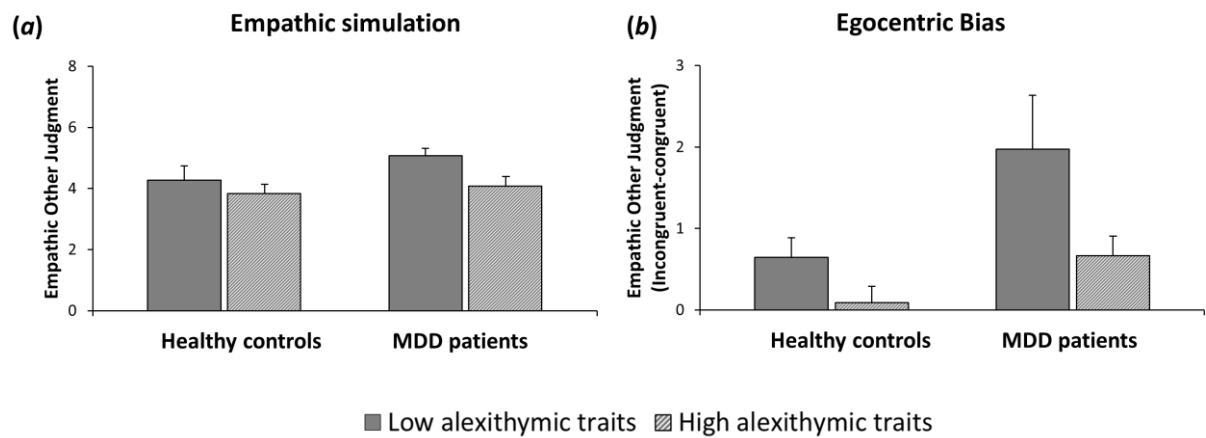


Figure 4.1. (a) Empathic simulation during simple condition (simple conditions). Depressed patients showed intact empathic simulation. Alexithymia decreased empathic simulation, independently of depression (b) Depressed patients showed an increased egocentric bias during empathic relating (Other incongruent – Other congruent) under the complex condition, independently of alexithymia. Alexithymia decreased the egocentric bias independently of depression.

To look specifically at an altercentric bias during emotional self judgments, we analysed the simultaneous self ratings separately. There was a significant main effect of alexithymia group ($F_{1, 64} = 5.484, p = 0.022, \eta_p^2 = 0.079$) and a significant congruency by depression group interaction ($F_{1, 64} = 12.498, p = 0.001, \eta_p^2 = 0.163$), but no significant congruency by alexithymia group interaction ($F_{1, 64} = 0.312, p = 0.578, \eta_p^2 = 0.005$). Additionally there was a marginal congruency by valence by depression group interaction ($F_{1, 64} = 3.897, p = 0.053, \eta_p^2 = 0.057$). There were no other significant main effects and interactions ($F_s < 2.060, p_s > .156$). Response inhibition as measured with the d-prime score, did not account for the increased altercentric bias in ($F_{1, 64} = 3.379, p = 0.071, \eta_p^2 = 0.050$). These results suggest that depressed patients show a significantly increased altercentric bias

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($F_{1, 66} = 13.489$, $p < 0.001$, $\eta_p^2 = 0.70$) during emotional self judgments, irrespective of alexithymia (see Figure 4.2a).

Egocentric bias and altercentric bias were correlated for both healthy controls ($r = .533$, $p < .001$) and depressed patients ($r = .658$, $p < .001$). There was a relationship between the egocentric bias and symptom severity ($r = -.408$, $p = .028$), which was accounted for by alexithymia (partial correlation: $r = -.105$, $p = .589$). The altercentric bias showed a positive association with the average length of the depressive episodes ($r = .479$, $p = .024$).

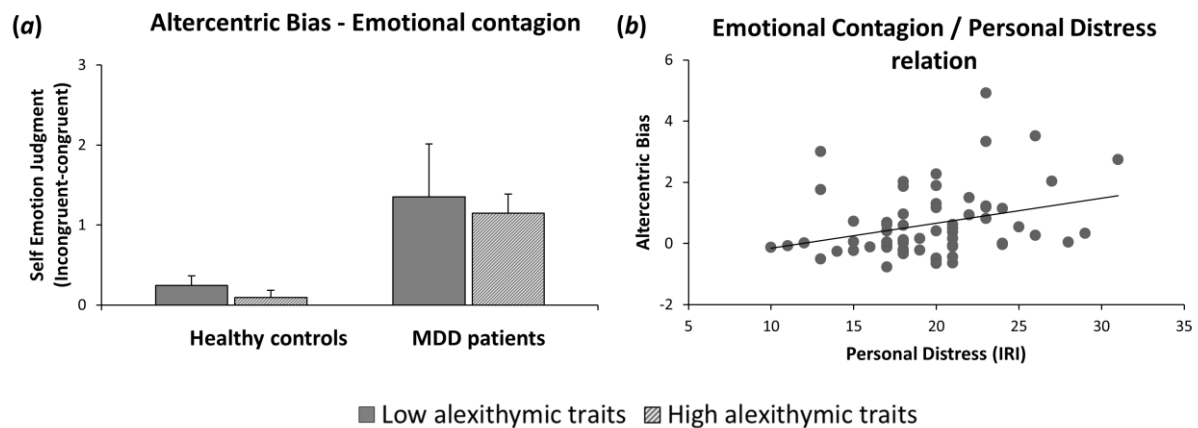


Figure 4.2. (a) Altercentric bias during emotional self judgments (Self incongruent – Self congruent), i.e. emotional contagion. MDD patients showed increased emotional contagion, unaffected by alexithymia. (b) Significant positive correlation over the entire sample between emotional contagion and personal distress as measured by the IRI.

Inhibitory control

To investigate differences in inhibitory control an ANCOVA with depression group and alexithymia group as between-subjects factors, as well as age, education and crystalline IQ as covariates was performed on the d-prime scores. There were no significant main effects of depression group ($F_{1, 64} = 0.005$, $p = 0.941$, $\eta_p^2 < 0.001$) and alexithymia group ($F_{1, 64} = 1.688$, $p = 0.198$, $\eta_p^2 = 0.026$), and no significant depression group by alexithymia group interaction ($F_{1, 64} = 0.238$, $p = 0.628$, $\eta_p^2 = 0.004$). These results showed that there were no differences in response inhibition between the groups.

Empathy trait measure

ANCOVAs on the different subscales of the IRI (empathic concern, perspective-taking, personal distress, fantasy) with depression group and alexithymia group as between-subjects factors as well as age, education and crystalline IQ as covariates were performed. Individuals with depression exhibited significantly more personal distress than healthy controls ($F_{1, 61} = 14.929$, $p < 0.001$, $\eta_p^2 = 0.197$). Individuals with high alexithymia also showed a tendency for more personal distress than individuals with low alexithymia ($F_{1, 61} = 3.040$, $p = 0.086$, $\eta_p^2 = 0.047$). Individuals with high alexithymia showed lower perspective-taking than individuals with low alexithymia ($F_{1, 61} = 9.527$, $p = 0.003$, $\eta_p^2 = 0.135$). There was a significant positive correlation over the entire sample of empathic distress (see Figure 4.2b) and empathic concern with the altercentric bias in the ETOP ($r = .312$, $p = .010$; $r = .242$, $p = .047$). Controlling personal distress and empathic concern against each other only the personal distress association with the altercentric bias remained.

Discussion

This study aimed to arrive at a more comprehensive picture of empathic relating in depression, in further elucidating the role of alexithymia while looking at empathic relating under simple and complex conditions, manipulating the congruency of emotional perspectives of self and other.

As hypothesized, we found that only alexithymia but not depression itself accounted for deficits in empathic relating under the simple condition, when simulation mechanisms suffice to arrive at an accurate empathic judgment of another persons' emotional perspective. This represents an important finding, suggesting intact empathic relating based on simulation in individuals with depression, when alexithymia is accounted for.

Looking at the complex condition, when emotional perspectives of self and other differ, depressed patients exhibited an increased egocentric bias during empathic relating under the complex condition suggesting that they have difficulties in detaching from their own egocentric perspective to empathically relate to the incongruent emotional perspective of the other. Previous studies linked increased egocentric bias during empathic relating in children to decreased functional coupling of IDLPFC with rSMG (Steinbeis et al., 2014) and emotional conflict processing deficits (Hoffmann et al., in press). Albeit speculative it could be suggested that also in depression, it is deficits particularly in emotional conflict resolution, possibly related to poor functioning of DLPFC, that explain increased egocentric bias during empathic relating in these participants. Deficits in emotional and non-emotional emotional conflict processing and DLPFC functioning have been commonly reported for depression (Etkin & Schatzberg, 2011; Grimm et al., 2008; C. F. Murphy et al., 2007; Siegle, Thompson, Carter, Steinhauer, & Thase, 2007; Waring et al., 2013; Wolkenstein et al, 2014). This would suggest that the egocentric bias during empathic relating in depression is not a problem of empathic relating as simulation processes are intact under simple conditions, but rather a problem of resolving conflicting emotional perspectives under more complex conditions.

Besides increased egocentric bias during empathic relating depressed patients also showed an increased altercentric bias during emotional self judgments, suggesting a heightened emotional contagion in this population. Indeed individual differences in personal distress across the entire sample correlated positively with the altercentric bias, indicating that part of the heightened emotional contagion can be attributed to high personal distress, which is commonly reported for depression (Schreiter & Pijnenborg, 2013). Interestingly the size of the emotional contagion in depressed patients, as measured by the altercentric bias was positively associated with the average length of the depressive episodes. The heightened emotional contagion to other's emotional perspectives, seems to somehow contribute to perpetuating the depressive state. Thus, this might represent a need in depressed patients to monitor the relationship with others, possibly related to previously described rejection sensitivity (Ayduk, Downey, & Kim, 2001; Tops, Riese, Oldehinkel, Rijdsdijk, & Ormel, 2008), insecure attachment patterns (Roberts, Gotlib, & Kassel, 1996), loss anticipation, and general threat detection (Gotlib, Krasnoperova, Yue, & Joormann, 2004).

Last we hypothesized that alexithymia would have a stronger affect on the egocentric bias during empathic judgments, than on emotional contagion. Indeed independently of depression individuals with high alexithymia showed a smaller egocentric bias during empathic judgments, but no changed emotional contagion. As alexithymia has been associated with decreased emotional awareness (Bird et al., 2010; Silani et al., 2008), it is likely that individuals with high alexithymia do not experience a strong emotional conflict and find it easier to detach from their own emotional perspective, while relating to the emotional perspective of another person. This could possibly relate to decreased functioning of the anterior insular within the empathy network (Silani et al., 2013; Steinbeis et al., 2014), which has been previously found to show decreased activation in alexithymia (Bird et al., 2010; Silani et al., 2008). In contrast emotional contagion was not modulated by alexithymia, which could be explained by the fact that emotional contagion is an automatic and seemingly

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unconscious process, less affected by the level of emotional awareness. Contributing to this explanation are the findings that personal distress is generally not decreased in individuals with high alexithymia, sometimes even increased as was found in this study. Other studies have indeed reported personal distress and emotional arousal in alexithymia, suggesting automatic emotional resonance is intact in individuals with high alexithymia (Grynberg, Luminet, Corneille, Grèzes, & Berthoz, 2010; Stone & Nielson, 2001; Taylor & Bagby, 2004)

Egocentric bias during empathic relating and emotional contagion showed a positive relation in our study. This might suggest that partly the same mechanism could underlie these two biases. While response inhibition did not show any association with the egocentric and altercentric biases, emotional conflict processing could represent a viable underlying mechanism, as suggested above. The role of emotional conflict processing in empathic relating of individuals with depression under complex conditions when self and other perspectives differ, should be further elucidated in future studies.

Lastly we had hypothesized valence-dependent effects, specifically under complex empathy conditions. Against our hypotheses, depressed patients also showed heightened egocentric bias, when they had to detach from their own positive perspective to take the negative perspective of the other. Depressed patients also showed stronger emotional contagion towards the positive emotional perspective of another. Considering the normally heightened processing of negative stimuli in depression, this finding was surprising. Egocentric and altercentric bias also showed a tendency to be stronger in healthy controls when a positive perspective had to be detached from, which could suggest that the positive stimuli, might have been more distracting in general.

The present findings represent an important step towards a more detailed description of empathic relating in depression and are consequentially of clinical relevance. Psychotherapeutic intervention heavily relies on building a therapeutic alliance between patient and psychotherapist that is based on empathic understanding. This study delivers

evidence that empathic relating based on simulation is intact in depressed patients, when no concurrent alexithymia is present. Alexithymia in depression thus will have negative effects on the development of a well-functioning therapeutic relationship and favorable therapeutic outcome (Ogrodniczuk, Piper, & Joyce, 2005; Sifneos, 1973). Independently of alexithymia, depressed patients tend to show difficulties during empathic relating under complex conditions, when emotional perspectives of self and other differ, while also showing heightened emotional contagion. These difficulties may thus be inherent to the depressive condition, and as suggested possibly related to emotional conflict processing abilities.

In conclusion, this study aimed to investigate empathic abilities in depression more fully in testing empathic relating under simple and complex conditions and its relation to alexithymia. Individuals with depression showed intact empathic relating based on simulation, when no alexithymia was present. In addition, independently of alexithymia, depressed patients showed increased egocentric bias during empathic relating under the complex condition, when emotional perspectives of self and other differed, as well as increased emotional contagion during emotional self judgments. These findings represent a crucial step forward in clarifying in what way, and under what circumstances individuals with depression do exhibit deficits in empathic relating, which will be of relevance for clinicians.

References

- Ayduk, O., Downey, G., & Kim, M. (2001). Rejection sensitivity and depressive symptoms in women. *Personality and Social Psychology Bulletin*, 27(7), 868-877.
- Bagby, R. M., Parker, J. D., & Taylor, G. J. (1994). The twenty-item Toronto Alexithymia Scale—I. Item selection and cross-validation of the factor structure. *Journal of psychosomatic research*, 38(1), 23-32.
- Bastiaansen, J., Thioux, M., & Keysers, C. (2009). Evidence for mirror systems in emotions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1528), 2391-2404.
- Berpohl, F., Walter, M., Sajonz, B., Lücke, C., Hägele, C., Sterzer, P., . . . Northoff, G. (2009). Attentional modulation of emotional stimulus processing in patients with major depression—alterations in prefrontal cortical regions. *Neuroscience letters*, 463(2), 108-113.
- Bird, G., & Cook, R. (2013). Mixed emotions: the contribution of alexithymia to the emotional symptoms of autism. *Translational Psychiatry*, 3(7). e285.
- Bird, G., Silani, G., Brindley, R., White, S., Frith, U., & Singer, T. (2010). Empathic brain responses in insula are modulated by levels of alexithymia but not autism. *Brain*, awq060.
- Brass, M., Ruby, P., & Spengler, S. (2009). Inhibition of imitative behaviour and social cognition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1528), 2359-2367.
- Davis, M. H. (1980). A multidimensional approach to individual differences in empathy. *JSAS, Catalog of Selected Documents in Psychology*, 10, 85-104.

- Decety, J., & Lamm, C. (2007). The role of the right temporoparietal junction in social interaction: how low-level computational processes contribute to meta-cognition. *The Neuroscientist*, 13(6), 580-593.
- Etkin, A., & Schatzberg, A. F. (2011). Common abnormalities and disorder-specific compensation during implicit regulation of emotional processing in generalized anxiety and major depressive disorders. *American Journal of Psychiatry*, 168(9), 968-978.
- Franz, M., Popp, K., Schaefer, R., Sitte, W., Schneider, C., Hardt, J., . . . Braehler, E. (2008). Alexithymia in the German general population. *Social psychiatry and psychiatric epidemiology*, 43(1), 54-62.
- Gallese, V. (2001). The 'shared manifold' hypothesis. From mirror neurons to empathy. *Journal of consciousness studies*, 8(5-7), 33-50.
- Gallese, V. (2007). Before and below 'theory of mind': embodied simulation and the neural correlates of social cognition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1480), 659-669.
- Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends in cognitive sciences*, 2(12), 493-501.
- Gotlib, I. H., Krasnoperova, E., Yue, D. N., & Joormann, J. (2004). Attentional biases for negative interpersonal stimuli in clinical depression. *Journal of abnormal psychology*, 113(1), 127.
- Grimm, S., Beck, J., Schuepbach, D., Hell, D., Boesiger, P., Bermpohl, F., . . . Northoff, G. (2008). Imbalance between left and right dorsolateral prefrontal cortex in major depression is linked to negative emotional judgment: an fMRI study in severe major depressive disorder. *Biological psychiatry*, 63(4), 369-376.

4. Manuscript of Study 3

- Grynberg, D., Luminet, O., Corneille, O., Grèzes, J., & Berthoz, S. (2010). Alexithymia in the interpersonal domain: A general deficit of empathy? *Personality and Individual Differences, 49*(8), 845-850.
- Hamilton, M. (1960). A rating scale for depression. *Journal of neurology, neurosurgery, and psychiatry, 23*(1), 56.
- Hautzinger, M., Bailer, M., Worall, H., & Keller, F. (1995). BDI Beck-Depressions-Inventar. *Bern: Verlag Hans Huber.*
- Hirschfeld, R., Montgomery, S. A., Keller, M. B., Kasper, S., Schatzberg, A. F., Möller, H.-J., . . . Versiani, M. (2000). Social functioning in depression: a review. *Journal of Clinical Psychiatry, 61*(4), 268-275.
- Hoffmann, F., Singer, T., & Steinbeis, N. (in press). Children's increased emotional egocentricity compared to adults is mediated by their difficulties in conflict processing. *Child development.*
- Honkalampi, K., Hintikka, J., Tanskanen, A., Lehtonen, J., & Viinamäki, H. (2000). Depression is strongly associated with alexithymia in the general population. *Journal of Psychosomatic Research, 48*(1), 99-104.
- Joormann, J., & Gotlib, I. H. (2010). Emotion regulation in depression: relation to cognitive inhibition. *Cognition and Emotion, 24*(2), 281-298.
- Kanske, P., Heissler, J., Schönfelder, S., & Wessa, M. (2012). Neural correlates of emotion regulation deficits in remitted depression: the influence of regulation strategy, habitual regulation use, and emotional valence. *Neuroimage, 61*(3), 686-693.
- Kanske, P., & Kotz, S. A. (2012). Effortful control, depression, and anxiety correlate with the influence of emotion on executive attentional control. *Biological Psychology, 91*(1), 88-95.
- Leppänen, J. M. (2006). Emotional information processing in mood disorders: a review of behavioral and neuroimaging findings. *Current Opinion in Psychiatry, 19*(1), 34-39.

- Mitchell, J. P. (2009). Inferences about mental states. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1521), 1309-1316.
- Moriguchi, Y., Decety, J., Ohnishi, T., Maeda, M., Mori, T., Nemoto, K., . . . Komaki, G. (2007). Empathy and judging other's pain: an fMRI study of alexithymia. *Cerebral Cortex*, 17(9), 2223-2234.
- Murphy, C. F., Gunning-Dixon, F. M., Hoptman, M. J., Lim, K. O., Ardekani, B., Shields, J. K., . . . Alexopoulos, G. S. (2007). White-matter integrity predicts stroop performance in patients with geriatric depression. *Biological psychiatry*, 61(8), 1007-1010.
- Murphy, F., Sahakian, B., Rubinsztein, J., Michael, A., Rogers, R., Robbins, T., & Paykel, E. (1999). Emotional bias and inhibitory control processes in mania and depression. *Psychological medicine*, 29(06), 1307-1321.
- Nickerson, R. S. (2001). The projective way of knowing: A useful heuristic that sometimes misleads. *Current Directions in Psychological Science*, 10(5), 168-172.
- Ogrodniczuk, J. S., Piper, W. E., & Joyce, A. S. (2005). The negative effect of alexithymia on the outcome of group therapy for complicated grief: what role might the therapist play? *Comprehensive psychiatry*, 46(3), 206-213.
- Paelecke-Habermann, Y., Pohl, J., & Leplow, B. (2005). Attention and executive functions in remitted major depression patients. *Journal of affective disorders*, 89(1), 125-135.
- Roberts, J. E., Gotlib, I. H., & Kassel, J. D. (1996). Adult attachment security and symptoms of depression: The mediating roles of dysfunctional attitudes and low self-esteem. *Journal of Personality and Social Psychology*, 70(2), 310-320.
- Schmidt, K.-H., & Metzler, P. (1992). *Wortschatztest: WST*: Beltz.
- Schreiter, S., & Pijnenborg, G. (2013). Empathy in adults with clinical or subclinical depressive symptoms. *Journal of affective disorders*, 150(1), 1-16.

4. Manuscript of Study 3

- Siegle, G. J., Thompson, W., Carter, C. S., Steinhauer, S. R., & Thase, M. E. (2007). Increased amygdala and decreased dorsolateral prefrontal BOLD responses in unipolar depression: related and independent features. *Biological psychiatry*, 61(2), 198-209.
- Sifneos, P. E. (1973). The prevalence of 'alexithymic' characteristics in psychosomatic patients. *Psychotherapy and psychosomatics*, 22(2-6), 255-262.
- Silani, G., Bird, G., Brindley, R., Singer, T., Frith, C., & Frith, U. (2008). Levels of emotional awareness and autism: an fMRI study. *Social Neuroscience*, 3(2), 97-112.
- Silani, G., Lamm, C., Ruff, C. C., & Singer, T. (2013). Right Supramarginal Gyrus Is Crucial to Overcome Emotional Egocentricity Bias in Social Judgments. *The Journal of Neuroscience*, 33(39), 15466-15476.
- Singer, T. (2012). The past, present and future of social neuroscience: A European perspective. *Neuroimage*, 61(2), 437-449.
- Singer, T., & Lamm, C. (2009). The social neuroscience of empathy. *Annals of the New York Academy of Sciences*, 1156(1), 81-96.
- Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R. J., & Frith, C. D. (2004). Empathy for pain involves the affective but not sensory components of pain. *Science*, 303(5661), 1157-1162.
- Steinbeis, N., Bernhardt, B. C., & Singer, T. (2014). Age-related differences in function and structure of rSMG and reduced functional connectivity with DLPFC explains heightened emotional egocentricity bias in childhood. *Social Cognitive and Affective Neuroscience*, nsu057.
- Sterzer, P., Hilgenfeldt, T., Freudenberg, P., Bermpohl, F., & Adli, M. (2011). Access of emotional information to visual awareness in patients with major depressive disorder. *Psychological medicine*, 41(08), 1615-1624.

- Stone, L. A., & Nielson, K. A. (2001). Intact physiological response to arousal with impaired emotional recognition in alexithymia. *Psychotherapy and psychosomatics*, 70(2), 92-102.
- Taylor, G. J., & Bagby, R. M. (2004). New trends in alexithymia research. *Psychotherapy and psychosomatics*, 73(2), 68-77.
- Thoma, P., Zalewski, I., von Reventlow, H. G., Norra, C., Juckel, G., & Daum, I. (2011). Cognitive and affective empathy in depression linked to executive control. *Psychiatry research*, 189(3), 373-378.
- Tops, M., Riese, H., Oldehinkel, A. J., Rijdsdijk, F. V., & Ormel, J. (2008). Rejection sensitivity relates to hypocortisolism and depressed mood state in young women. *Psychoneuroendocrinology*, 33(5), 551-559.
- Van Boven, L., & Loewenstein, G. (2003). Social projection of transient drive states. *Personality and Social Psychology Bulletin*, 29(9), 1159-1168.
- Waring, J. D., Etkin, A., Hallmayer, J. F., & O'Hara, R. (2013). Connectivity Underlying Emotion Conflict Regulation in Older Adults with 5-HTTLPR Short Allele: A Preliminary Investigation. *The American journal of geriatric psychiatry: official journal of the American Association for Geriatric Psychiatry*, 22, 946-950.
- Wilbertz, G., Brakemeier, E.-L., Zobel, I., Härter, M., & Schramm, E. (2010). Exploring preoperational features in chronic depression. *Journal of affective disorders*, 124(3), 262-269.
- Wittchen, H.-U., Wunderlich, U., Gruschwitz, S., & Zaudig, M. (1997). Skid-i. *Strukturiertes Klinisches Interview für DSM-IV*.
- Wolkenstein, L., Schönenberg, M., Schirm, E., & Hautzinger, M. (2011). I can see what you feel, but I can't deal with it: Impaired theory of mind in depression. *Journal of affective disorders*, 132(1), 104-111.

4. Manuscript of Study 3

Wolkenstein, L., Zeiller, M., Kanske, P., & Plewnia, C. (2014). Induction of a depression-like negativity bias by cathodal transcranial direct current stimulation. *Cortex*, 59, 103-112.

Bibliography

- Aichhorn, M., Perner, J., Kronbichler, M., Staffen, W., & Ladurner, G. (2006). Do visual perspective tasks need theory of mind? *Neuroimage*, 30(3), 1059-1068.
- Apperly, I. A., Warren, F., Andrews, B. J., Grant, J., & Todd, S. (2011). Developmental continuity in theory of mind: Speed and accuracy of belief–desire reasoning in children and adults. *Child development*, 82(5), 1691-1703.
- Asperger, H. (1944). Die „Autistischen Psychopathen“ im Kindesalter. *European Archives of Psychiatry and Clinical Neuroscience*, 117(1), 76-136.
- American Psychiatric Association. (2000). *Diagnostic and Statistical Manual of Mental Disorders, text revision* (4th ed., text rev.). Washington, DC : American Psychiatric Association.
- American Psychiatric Association. (2013). *Diagnostic and Statistical Manual of Mental Disorders* (5th ed.). Arlington,VA: American Psychiatric Association.
- Ayduk, O., Downey, G., & Kim, M. (2001). Rejection sensitivity and depressive symptoms in women. *Personality and Social Psychology Bulletin*, 27(7), 868-877.
- Badre, D., & Wagner, A. D. (2004). Selection, integration, and conflict monitoring: assessing the nature and generality of prefrontal cognitive control mechanisms. *Neuron*, 41(3), 473-487.
- Bagby, R. M., Parker, J. D., & Taylor, G. J. (1994). The twenty-item Toronto Alexithymia Scale—I. Item selection and cross-validation of the factor structure. *Journal of psychosomatic research*, 38(1), 23-32.
- Baron-Cohen, S., Leslie, A. M., & Frith, U. (1985). Does the autistic child have a “theory of mind”? *Cognition*, 21(1), 37-46.

Bibliography

- Baron - Cohen, S., Wheelwright, S., Hill, J., Raste, Y., & Plumb, I. (2001). The “Reading the mind in the eyes” test revised version: A study with normal adults, and adults with asperger syndrome or high - functioning autism. *Journal of Child Psychology and Psychiatry*, 42(2), 241-251.
- Baron, R. M., & Kenny, D. A. (1986). The moderator–mediator variable distinction in social psychological research: Conceptual, strategic, and statistical considerations. *Journal of personality and social psychology*, 51(6), 1173-1182.
- Bastiaansen, J., Thioux, M., & Keysers, C. (2009). Evidence for mirror systems in emotions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1528), 2391-2404.
- Batson, C. D. (2009). These things called empathy: eight related but distinct phenomena.
- Batson, C. D., & Shaw, L. L. (1991). Evidence for altruism: Toward a pluralism of prosocial motives. *Psychological Inquiry*, 2(2), 107-122.
- Begeer, S., Bernstein, D. M., van Wijhe, J., Scheeren, A. M., & Koot, H. M. (2012). A continuous false belief task reveals egocentric biases in children and adolescents with Autism Spectrum Disorders. *Autism*, 16(4), 357-366.
- Bellah, R. N., Madsen, R., Sullivan, W. M., Swidler, A., & Tipton, S. M. (1985). Habits of the heart: Individualism and commitment in American life.
- Belmonte, M. K., Allen, G., Beckel-Mitchener, A., Boulanger, L. M., Carper, R. A., & Webb, S. J. (2004). Autism and abnormal development of brain connectivity. *The Journal of Neuroscience*, 24(42), 9228-9231.
- Benabou, R., & Tirole, J. (2003). Intrinsic and extrinsic motivation. *The Review of Economic Studies*, 70(3), 489-520.
- Bermpohl, F., Walter, M., Sajonz, B., Lücke, C., Hägele, C., Sterzer, P., . . . Northoff, G. (2009). Attentional modulation of emotional stimulus processing in patients with

- major depression—alterations in prefrontal cortical regions. *Neuroscience letters*, 463(2), 108-113.
- Birch, S. A., & Bloom, P. (2007). The curse of knowledge in reasoning about false beliefs. *Psychological Science*, 18(5), 382-386.
- Bird, G., & Cook, R. (2013). Mixed emotions: the contribution of alexithymia to the emotional symptoms of autism. *Translational Psychiatry*, 3(7). e285.
- Bird, G., Silani, G., Brindley, R., White, S., Frith, U., & Singer, T. (2010). Empathic brain responses in insula are modulated by levels of alexithymia but not autism. *Brain*, 133(5), 1515-1525.
- Blair, R. J. R., Peschardt, K., Budhani, S., Mitchell, D., & Pine, D. (2006). The development of psychopathy. *Journal of Child Psychology and Psychiatry*, 47(3 - 4), 262-276.
- Blakemore, S.-J., & Decety, J. (2001). From the perception of action to the understanding of intention. *Nature Reviews Neuroscience*, 2(8), 561-567.
- Bohl, V., & van den Bos, W. (2012). Toward an integrative account of social cognition: marrying theory of mind and interactionism to study the interplay of Type 1 and Type 2 processes. *Frontiers in human neuroscience*, 6(274), 11.
- Brass, M., Ruby, P., & Spengler, S. (2009). Inhibition of imitative behaviour and social cognition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1528), 2359-2367.
- Brüne, M. (2005). "Theory of mind" in schizophrenia: a review of the literature. *Schizophrenia bulletin*, 31(1), 21-42.
- Brüne, M., & Brüne-Cohrs, U. (2006). Theory of mind—evolution, ontogeny, brain mechanisms and psychopathology. *Neuroscience & Biobehavioral Reviews*, 30(4), 437-455.
- Buckner, R. L., Andrews - Hanna, J. R., & Schacter, D. L. (2008). The brain's default network. *Annals of the New York Academy of Sciences*, 1124(1), 1-38.

Bibliography

- Burns, D. D., & Nolen-Hoeksema, S. (1992). Therapeutic empathy and recovery from depression in cognitive-behavioral therapy: a structural equation model. *Journal of Consulting and Clinical Psychology*, 60(3), 441-449.
- Bzdok, D., Langner, R., Schilbach, L., Jakobs, O., Roski, C., Caspers, S., . . . Eickhoff, S. B. (2013). Characterization of the temporo-parietal junction by combining data-driven parcellation, complementary connectivity analyses, and functional decoding. *Neuroimage*, 81, 381-392.
- Carlson, S. M., & Moses, L. J. (2001). Individual differences in inhibitory control and children's theory of mind. *Child development*, 72(4), 1032-1053.
- Carter, R. M., & Huettel, S. A. (2013). A nexus model of the temporal–parietal junction. *Trends in cognitive sciences*, 17(7), 328-336.
- Castelli, F., Frith, C., Happé, F., & Frith, U. (2002). Autism, Asperger syndrome and brain mechanisms for the attribution of mental states to animated shapes. *Brain*, 125(8), 1839-1849.
- Chen, Q., Wei, P., & Zhou, X. (2006). Distinct neural correlates for resolving stroop conflict at inhibited and noninhibited locations in inhibition of return. *Journal of cognitive neuroscience*, 18(11), 1937-1946.
- Chevallier, C., Kohls, G., Troiani, V., Brodtkin, E. S., & Schultz, R. T. (2012). The social motivation theory of autism. *Trends in cognitive sciences*, 16(4), 231-239.
- Cook, R., Bird, G., Catmur, C., Press, C., & Heyes, C. (2014). Mirror neurons: from origin to function. *Behavioral and Brain Sciences*, 37(02), 177-192.
- Courchesne, E., & Pierce, K. (2005). Why the frontal cortex in autism might be talking only to itself: local over-connectivity but long-distance disconnection. *Current Opinion in Neurobiology*, 15(2), 225-230.
- Csibra, G., & Gergely, G. (2007). ‘Obsessed with goals’: Functions and mechanisms of teleological interpretation of actions in humans. *Acta Psychologica*, 124(1), 60-78.

- Dapretto, M., Davies, M. S., Pfeifer, J. H., Scott, A. A., Sigman, M., Bookheimer, S. Y., & Iacoboni, M. (2005). Understanding emotions in others: mirror neuron dysfunction in children with autism spectrum disorders. *Nature neuroscience*, 9(1), 28-30.
- David, N., Schultz, J., Milne, E., Schunke, O., Schöttle, D., Münchau, A., . . . Engel, A. K. (2013). Right Temporoparietal Gray Matter Predicts Accuracy of Social Perception in the Autism Spectrum. *Journal of Autism and Developmental Disorders*, 1-14.
- Davis, M. H. (1980). A multidimensional approach to individual differences in empathy. *JSAS, Catalog of Selected Documents in Psychology*, 10, 85-104.
- Deary, I. J., Der, G., & Ford, G. (2001). Reaction times and intelligence differences: A population-based cohort study. *Intelligence*, 29(5), 389-399.
- Decety, J., & Lamm, C. (2007). The role of the right temporoparietal junction in social interaction: how low-level computational processes contribute to meta-cognition. *The Neuroscientist*, 13(6), 580-593.
- Decety, J., & Meyer, M. (2008). From emotion resonance to empathic understanding: A social developmental neuroscience account. *Development and psychopathology*, 20(04), 1053-1080.
- Decety, J., & Sommerville, J. A. (2003). Shared representations between self and other: a social cognitive neuroscience view. *Trends in cognitive sciences*, 7(12), 527-533.
- Di Martino, A., Yan, C. G., Li, Q., Denio, E., Castellanos, F. X., Alaerts, K., . . . Milham, M. P. (2013). The autism brain imaging data exchange: towards a large-scale evaluation of the intrinsic brain architecture in autism. *Molecular Psychiatry*, 19, 659-667.
- Dinstein, I., Hasson, U., Rubin, N., & Heeger, D. J. (2007). Brain areas selective for both observed and executed movements. *Journal of Neurophysiology*, 98(3), 1415-1427.
- Dziobek, I., Fleck, S., Kalbe, E., Rogers, K., Hassenstab, J., Brand, M., . . . Convit, A. (2006). Introducing MASC: a movie for the assessment of social cognition. *Journal of autism and developmental disorders*, 36(5), 623-636.

Bibliography

- Dziobek, I., Rogers, K., Fleck, S., Bahnemann, M., Heekeren, H. R., Wolf, O. T., & Convit, A. (2008). Dissociation of cognitive and emotional empathy in adults with Asperger syndrome using the Multifaceted Empathy Test (MET). *Journal of Autism and Developmental Disorders*, 38(3), 464-473.
- Egner, T., Etkin, A., Gale, S., & Hirsch, J. (2008). Dissociable neural systems resolve conflict from emotional versus nonemotional distracters. *Cerebral Cortex*, 18(6), 1475-1484.
- Egner, T., & Hirsch, J. (2005). Cognitive control mechanisms resolve conflict through cortical amplification of task-relevant information. *Nature neuroscience*, 8(12), 1784-1790.
- Eisenberg, N. (2000). Emotion, regulation, and moral development. *Annual review of psychology*, 51(1), 665-697.
- Eisenberg, N., Fabes, R. A., Miller, P. A., Fultz, J., Shell, R., Mathy, R. M., & Reno, R. R. (1989). Relation of sympathy and personal distress to prosocial behavior: a multimethod study. *Journal of personality and social psychology*, 57(1), 55-66.
- Eisenberg, N., Shell, R., Pasternack, J., Lennon, R., Beller, R., & Mathy, R. M. (1987). Prosocial development in middle childhood: A longitudinal study. *Developmental psychology*, 23(5), 712-718.
- Elkind, D. (1967). Egocentrism in adolescence. *Child Development*, 1025-1034.
- Epley, N., Morewedge, C. K., & Keysar, B. (2004). Perspective taking in children and adults: Equivalent egocentrism but differential correction. *Journal of Experimental Social Psychology*, 40(6), 760-768.
- Eriksen, B. A., & Eriksen, C. W. (1974). Effects of noise letters upon the identification of a target letter in a nonsearch task. *Perception & psychophysics*, 16(1), 143-149.
- Etkin, A., Egner, T., Peraza, D. M., Kandel, E. R., & Hirsch, J. (2006). Resolving emotional conflict: a role for the rostral anterior cingulate cortex in modulating activity in the amygdala. *Neuron*, 51(6), 871-882.

- Etkin, A., & Schatzberg, A. F. (2011). Common abnormalities and disorder-specific compensation during implicit regulation of emotional processing in generalized anxiety and major depressive disorders. *American Journal of Psychiatry*, 168(9), 968-978.
- Etzel, J. A., Gazzola, V., & Keysers, C. (2008). Testing simulation theory with cross-modal multivariate classification of fMRI data. *PLOS ONE*, 3(11), e3690.
- Farb, N. A., Segal, Z. V., & Anderson, A. K. (2012). Mindfulness meditation training alters cortical representations of interoceptive attention. *Social Cognitive and Affective Neuroscience*, nss066.
- Fenske, M. J., & Eastwood, J. D. (2003). Modulation of focused attention by faces expressing emotion: evidence from flanker tasks. *Emotion*, 3(4), 327-343. doi: 10.1037/1528-3542.3.4.327
- Fjell, A. M., Walhovd, K. B., Brown, T. T., Kuperman, J. M., Chung, Y., Hagler, D. J., . . . McCabe, C. (2012). Multimodal imaging of the self-regulating developing brain. *Proceedings of the National Academy of Sciences*, 109(48), 19620-19625.
- Flavell, J. H. (1999). Cognitive development: Children's knowledge about the mind. *Annual review of psychology*, 50(1), 21-45.
- Flavell, J. H., Everett, B. A., Croft, K., & Flavell, E. R. (1981). Young children's knowledge about visual perception: Further evidence for the Level 1–Level 2 distinction. *Developmental psychology*, 17(1), 99-103.
- Franz, M., Popp, K., Schaefer, R., Sitte, W., Schneider, C., Hardt, J., . . . Braehler, E. (2008). Alexithymia in the German general population. *Social psychiatry and psychiatric epidemiology*, 43(1), 54-62.
- Friedman, O., & Leslie, A. M. (2005). Processing demands in belief - desire reasoning: inhibition or general difficulty? *Developmental Science*, 8(3), 218-225.
- Frith, C. D., & Frith, U. (2006). The neural basis of mentalizing. *Neuron*, 50(4), 531-534.

Bibliography

- Frith, C. D., & Frith, U. (2012). Mechanisms of social cognition. *Annual review of psychology*, 63, 287-313.
- Gallagher, S. (2001). The practice of mind. Theory, simulation or primary interaction? *Journal of Consciousness Studies*, 8(5-7), 5-7.
- Gallese, V. (2001). The 'shared manifold' hypothesis. From mirror neurons to empathy. *Journal of consciousness studies*, 8(5-7), 33-50.
- Gallese, V. (2007). Before and below 'theory of mind': embodied simulation and the neural correlates of social cognition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1480), 659-669.
- Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends in cognitive sciences*, 2(12), 493-501.
- Gazzola, V., Aziz-Zadeh, L., & Keysers, C. (2006). Empathy and the somatotopic auditory mirror system in humans. *Current Biology*, 16(18), 1824-1829.
- Geschwind, D. H., & Levitt, P. (2007). Autism spectrum disorders: developmental disconnection syndromes. *Current Opinion in Neurobiology*, 17(1), 103-111.
- Gogtay, N., Giedd, J. N., Lusk, L., Hayashi, K. M., Greenstein, D., Vaituzis, A. C., . . . Toga, A. W. (2004). Dynamic mapping of human cortical development during childhood through early adulthood. *Proceedings of the National Academy of Sciences of the United States of America*, 101(21), 8174-8179.
- Gotlib, I. H., Krasnoperova, E., Yue, D. N., & Joormann, J. (2004). Attentional biases for negative interpersonal stimuli in clinical depression. *Journal of abnormal psychology*, 113(1), 127.
- Green, B. G., Dalton, P., Cowart, B., Shaffer, G., Rankin, K., & Higgins, J. (1996). Evaluating the 'Labeled Magnitude Scale' for measuring sensations of taste and smell. *Chemical Senses*, 21(3), 323-334.

- Grimm, S., Beck, J., Schuepbach, D., Hell, D., Boesiger, P., Bermpohl, F., . . . Northoff, G. (2008). Imbalance between left and right dorsolateral prefrontal cortex in major depression is linked to negative emotional judgment: an fMRI study in severe major depressive disorder. *Biological psychiatry*, 63(4), 369-376.
- Gross, J. J. (2002). Emotion regulation: Affective, cognitive, and social consequences. *Psychophysiology*, 39(3), 281-291.
- Grynberg, D., Luminet, O., Corneille, O., Grèzes, J., & Berthoz, S. (2010). Alexithymia in the interpersonal domain: A general deficit of empathy? *Personality and Individual Differences*, 49(8), 845-850.
- Gusnard, D. A., Akbudak, E., Shulman, G. L., & Raichle, M. E. (2001). Medial prefrontal cortex and self-referential mental activity: relation to a default mode of brain function. *Proceedings of the National Academy of Sciences*, 98(7), 4259-4264.
- Hadjikhani, N., Zürcher, N., Rogier, O., Hippolyte, L., Lemonnier, E., Ruest, T., . . . Billstedt, E. (2014). Emotional contagion for pain is intact in autism spectrum disorders. *Translational psychiatry*, 4(1), e343.
- Hamilton, A. F. d. C., Brindley, R., & Frith, U. (2009). Visual perspective taking impairment in children with autistic spectrum disorder. *Cognition*, 113(1), 37-44.
- Hamilton, M. (1960). A rating scale for depression. *Journal of neurology, neurosurgery, and psychiatry*, 23(1), 56.
- Hansen Lagattuta, K., Sayfan, L., & Harvey, C. (2013). Beliefs About Thought Probability: Evidence for Persistent Errors in Mindreading and Links to Executive Control. *Child development*, 85(2), 659-674.
- Happé, F. G. (1994). An advanced test of theory of mind: Understanding of story characters' thoughts and feelings by able autistic, mentally handicapped, and normal children and adults. *Journal of Autism and Developmental Disorders*, 24(2), 129-154.

Bibliography

- Hare, T. A., Tottenham, N., Galvan, A., Voss, H. U., Glover, G. H., & Casey, B. (2008). Biological substrates of emotional reactivity and regulation in adolescence during an emotional go-nogo task. *Biological psychiatry*, 63(10), 927-934.
- Hautzinger, M., Bailer, M., Worall, H., & Keller, F. (1995). BDI Beck-Depressions-Inventar. *Bern: Verlag Hans Huber*.
- Hein, G., Lamm, C., Brodbeck, C., & Singer, T. (2011). Skin conductance response to the pain of others predicts later costly helping. *PloS one*, 6(8), e22759.
- Hein, G., Silani, G., Preuschoff, K., Batson, C. D., & Singer, T. (2010). Neural responses to ingroup and outgroup members' suffering predict individual differences in costly helping. *Neuron*, 68(1), 149-160.
- Heyes, C. (2010). Where do mirror neurons come from? *Neuroscience & Biobehavioral Reviews*, 34(4), 575-583.
- Hirschfeld, R., Montgomery, S. A., Keller, M. B., Kasper, S., Schatzberg, A. F., Möller, H.-J., . . . Versiani, M. (2000). Social functioning in depression: a review. *Journal of Clinical Psychiatry*, 61(4), 268-275.
- Hoffmann, F., Singer, T., & Steinbeis, N. (in press). Children's increased emotional egocentricity compared to adults is mediated by their difficulties in conflict processing. *Child development*.
- Hofmann, S. G., Sawyer, A. T., Witt, A. A., & Oh, D. (2010). The effect of mindfulness-based therapy on anxiety and depression: A meta-analytic review. *Journal of Consulting and Clinical Psychology*, 78(2), 169.
- Hölzel, B. K., Lazar, S. W., Gard, T., Schuman-Olivier, Z., Vago, D. R., & Ott, U. (2011). How does mindfulness meditation work? Proposing mechanisms of action from a conceptual and neural perspective. *Perspectives on Psychological Science*, 6(6), 537-559.

- Hölzel, B. K., Ott, U., Hempel, H., Hackl, A., Wolf, K., Stark, R., & Vaitl, D. (2007). Differential engagement of anterior cingulate and adjacent medial frontal cortex in adept meditators and non-meditators. *Neuroscience Letters*, 421(1), 16-21.
- Honkalampi, K., Hintikka, J., Tanskanen, A., Lehtonen, J., & Viinamäki, H. (2000). Depression is strongly associated with alexithymia in the general population. *Journal of Psychosomatic Research*, 48(1), 99-104.
- Horn, W. (1962). Leistungsprüfsystem, LPS: Handanweisung für die Durchführung, Auswertung und Interpretation.
- Hume, D. (1739/1978). *A treatise of human nature*. Oxford: Clarendon Press.
- Inoue, Y., Tonooka, Y., Yamada, K., & Kanba, S. (2004). Deficiency of theory of mind in patients with remitted mood disorder. *Journal of Affective Disorders*, 82(3), 403-409.
- Jabbi, M., Swart, M., & Keysers, C. (2007). Empathy for positive and negative emotions in the gustatory cortex. *Neuroimage*, 34(4), 1744-1753.
- Jones, A. P., Happé, F. G., Gilbert, F., Burnett, S., & Viding, E. (2010). Feeling, caring, knowing: different types of empathy deficit in boys with psychopathic tendencies and autism spectrum disorder. *Journal of Child Psychology and Psychiatry*, 51(11), 1188-1197.
- Joormann, J., & Gotlib, I. H. (2010). Emotion regulation in depression: relation to cognitive inhibition. *Cognition and Emotion*, 24(2), 281-298.
- Just, M. A., Cherkassky, V. L., Keller, T. A., Kana, R. K., & Minshew, N. J. (2007). Functional and anatomical cortical underconnectivity in autism: evidence from an FMRI study of an executive function task and corpus callosum morphometry. *Cerebral Cortex*, 17(4), 951-961.
- Just, M. A., Keller, T. A., Malave, V. L., Kana, R. K., & Varma, S. (2012). Autism as a neural systems disorder: a theory of frontal-posterior underconnectivity. *Neuroscience & Biobehavioral Reviews*, 36(4), 1292-1313.

Bibliography

- Kail, R. (1991). Developmental change in speed of processing during childhood and adolescence. *Psychological bulletin*, 109(3), 490-501.
- Kana, R. K., Libero, L. E., Hu, C. P., Deshpande, H. D., & Colburn, J. S. (2012). Functional Brain Networks and White Matter Underlying Theory-of-Mind in Autism. *Social Cognitive and Affective Neuroscience*, 9(1), 98-105.
- Kanfer, R., & Ackerman, P. L. (1989). Motivation and cognitive abilities: An integrative/aptitude-treatment interaction approach to skill acquisition. *Journal of applied psychology*, 74(4), 657.
- Kanske, P., Heissler, J., Schönfelder, S., & Wessa, M. (2012). Neural correlates of emotion regulation deficits in remitted depression: the influence of regulation strategy, habitual regulation use, and emotional valence. *Neuroimage*, 61(3), 686-693.
- Kanske, P., & Kotz, S. A. (2012). Effortful control, depression, and anxiety correlate with the influence of emotion on executive attentional control. *Biological Psychology*, 91(1), 88-95.
- Keysar, B., Lin, S., & Barr, D. J. (2003). Limits on theory of mind use in adults. *Cognition*, 89(1), 25-41.
- Kim, C., Kroger, J. K., & Kim, J. (2011). A functional dissociation of conflict processing within anterior cingulate cortex. *Human brain mapping*, 32(2), 304-312.
- Klin, A. (2000). Attributing social meaning to ambiguous visual stimuli in higher - functioning autism and Asperger syndrome: the Social Attribution Task. *Journal of Child Psychology and Psychiatry*, 41(7), 831-846.
- Kohlberg, L. (1976). Moral stages and moralization: The cognitive-developmental approach. *Moral development and behavior: Theory, research, and social issues*, 31-53.
- Lambert, M. J., & Barley, D. E. (2001). Research summary on the therapeutic relationship and psychotherapy outcome. *Psychotherapy: Theory, Research, Practice, Training*, 38(4), 357.

- Lamm, C., Decety, J., & Singer, T. (2011). Meta-analytic evidence for common and distinct neural networks associated with directly experienced pain and empathy for pain. *Neuroimage*, 54(3), 2492-2502.
- Lehrl, S., Triebig, G., & Fischer, B. (1995). Multiple choice vocabulary test MWT as a valid and short test to estimate premorbid intelligence. *Acta Neurologica Scandinavica*, 91(5), 335-345.
- Leppänen, J. M. (2006). Emotional information processing in mood disorders: a review of behavioral and neuroimaging findings. *Current Opinion in Psychiatry*, 19(1), 34-39.
- Lévesque, J., Eugène, F., Joannette, Y., Paquette, V., Mensour, B., Beaudoin, G., . . . Beauguard, M. (2003). Neural circuitry underlying voluntary suppression of sadness. *Biological psychiatry*, 53(6), 502-510.
- Li, S.-C., Lindenberger, U., Hommel, B., Aschersleben, G., Prinz, W., & Baltes, P. B. (2004). Transformations in the couplings among intellectual abilities and constituent cognitive processes across the life span. *Psychological Science*, 15(3), 155-163.
- Lipps, T. (1903). *Einfühlung, innere Nachahmung, und Organempfindungen*: Archiv für Psychologie.
- Lockwood, P. L., Bird, G., Bridge, M., & Viding, E. (2013). Dissecting empathy: high levels of psychopathic and autistic traits are characterized by difficulties in different social information processing domains. *Frontiers in human neuroscience*, 7, 760.
- Lombardo, M. V., & Baron-Cohen, S. (2011). The role of the self in mindblindness in autism. *Consciousness and cognition*, 20(1), 130-140.
- Lombardo, M. V., Chakrabarti, B., Bullmore, E. T., & Baron-Cohen, S. (2011). Specialization of right temporo-parietal junction for mentalizing and its relation to social impairments in autism. *Neuroimage*, 56(3), 1832-1838.
- Lord, C., Risi, S., Lambrecht, L., Cook, E. H., Leventhal, B. L., DiLavore, P. C., . . . Rutter, M. (2000). The Autism Diagnostic Observation Schedule-Generic: A standard measure

Bibliography

- of social and communication deficits associated with the spectrum of autism. *Journal of Autism and Developmental Disorders*, 30, 205-223.
- Lord, C., Rutter, M., & Le Couteur, A. (1994). Autism Diagnostic Interview-Revisited: a revised version of a diagnostic interview for caregivers of individuals with possible pervasive developmental disorders. *Journal of Autism and Developmental Disorders*, 24(5), 659-685.
- Luna, B., Garver, K. E., Urban, T. A., Lazar, N. A., & Sweeney, J. A. (2004). Maturation of cognitive processes from late childhood to adulthood. *Child development*, 75(5), 1357-1372.
- Malti, T., Gummerum, M., Keller, M., & Buchmann, M. (2009). Children's moral motivation, sympathy, and prosocial behavior. *Child development*, 80(2), 442-460.
- Mar, R. A. (2011). The neural bases of social cognition and story comprehension. *Annual review of psychology*, 62, 103-134.
- Mars, R. B., Sallet, J., Schüffelgen, U., Jbabdi, S., Toni, I., & Rushworth, M. F. (2012). Connectivity-based subdivisions of the human right "temporoparietal junction area": evidence for different areas participating in different cortical networks. *Cerebral Cortex*, 22(8), 1894-1903.
- McRae, K., Gross, J. J., Weber, J., Robertson, E. R., Sokol-Hessner, P., Ray, R. D., . . . Ochsner, K. N. (2012). The development of emotion regulation: an fMRI study of cognitive reappraisal in children, adolescents and young adults. *Social Cognitive and Affective Neuroscience*, 7(1), 11-22.
- Meltzoff, A. N., & Decety, J. (2003). What imitation tells us about social cognition: a rapprochement between developmental psychology and cognitive neuroscience. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 358(1431), 491-500.

- Merleau-Ponty, M. (1962). *Phenomenology of perception*, trans. C. Smith: London: Routledge.
- Minio-Paluello, I., Baron-Cohen, S., Avenanti, A., Walsh, V., & Aglioti, S. M. (2009). Absence of embodied empathy during pain observation in Asperger syndrome. *Biological psychiatry*, 65(1), 55-62.
- Mitchell, J. P. (2008). Activity in right temporo-parietal junction is not selective for theory-of-mind. *Cerebral Cortex*, 18(2), 262-271.
- Mitchell, J. P. (2009). Inferences about mental states. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1521), 1309-1316. doi: 10.1098/rstb.2008.0318
- Moll, H., & Tomasello, M. (2006). Level 1 perspective - taking at 24 months of age. *British Journal of Developmental Psychology*, 24(3), 603-613.
- Montag, C., Dziobek, I., Richter, I. S., Neuhaus, K., Lehmann, A., Sylla, R., . . . Gallinat, J. (2011). Different aspects of theory of mind in paranoid schizophrenia: evidence from a video-based assessment. *Psychiatry research*, 186(2), 203-209.
- Montag, C., Ehrlich, A., Neuhaus, K., Dziobek, I., Heekeren, H. R., Heinz, A., & Gallinat, J. (2010). Theory of mind impairments in euthymic bipolar patients. *Journal of Affective Disorders*, 123(1), 264-269.
- Moriguchi, Y., Decety, J., Ohnishi, T., Maeda, M., Mori, T., Nemoto, K., . . . Komaki, G. (2007). Empathy and judging other's pain: an fMRI study of alexithymia. *Cerebral Cortex*, 17(9), 2223-2234.
- Mueller, S., Keeser, D., Samson, A. C., Kirsch, V., Blautzik, J., Grothe, M., . . . Reiser, M. F. (2013). Convergent Findings of Altered Functional and Structural Brain Connectivity in Individuals with High Functioning Autism: A Multimodal MRI Study. *PLOS ONE*, 8(6), e67329.

Bibliography

- Murphy, C. F., Gunning-Dixon, F. M., Hoptman, M. J., Lim, K. O., Ardekani, B., Shields, J. K., . . . Alexopoulos, G. S. (2007). White-matter integrity predicts stroop performance in patients with geriatric depression. *Biological psychiatry*, 61(8), 1007-1010.
- Murphy, F., Sahakian, B., Rubinsztein, J., Michael, A., Rogers, R., Robbins, T., & Paykel, E. (1999). Emotional bias and inhibitory control processes in mania and depression. *Psychological medicine*, 29(06), 1307-1321.
- Newcomb, A. F., Bukowski, W. M., & Pattee, L. (1993). Children's peer relations: a meta-analytic review of popular, rejected, neglected, controversial, and average sociometric status. *Psychological bulletin*, 113(1), 99-128.
- Nickerson, R. S. (2001). The projective way of knowing: A useful heuristic that sometimes misleads. *Current Directions in Psychological Science*, 10(5), 168-172.
- Northoff, G. (2007). Psychopathology and pathophysiology of the self in depression—neuropsychiatric hypothesis. *Journal of affective disorders*, 104(1), 1-14.
- O'doherty, J., Rolls, E., Francis, S., Bowtell, R., & McGlone, F. (2001). Representation of pleasant and aversive taste in the human brain. *Journal of neurophysiology*, 85(3), 1315-1321.
- O'Brien, E., & Ellsworth, P. C. (2012). More Than Skin Deep Visceral States Are Not Projected Onto Dissimilar Others. *Psychological Science*, 23(4), 391-396.
- Ogrodniczuk, J. S., Piper, W. E., & Joyce, A. S. (2005). The negative effect of alexithymia on the outcome of group therapy for complicated grief: what role might the therapist play? *Comprehensive psychiatry*, 46(3), 206-213.
- Paelecke-Habermann, Y., Pohl, J., & Lepow, B. (2005). Attention and executive functions in remitted major depression patients. *Journal of affective disorders*, 89(1), 125-135.
- Paris, J. (2014). Modernity and narcissistic personality disorder. *Personality Disorders: Theory, Research, and Treatment*, 5(2), 220.

- Paul, N. A., Stanton, S. J., Greeson, J. M., Smoski, M. J., & Wang, L. (2013). Psychological and neural mechanisms of trait mindfulness in reducing depression vulnerability. *Social Cognitive and Affective Neuroscience*, 8(1), 56-64.
- Perner, J., & Lang, B. (1999). Development of theory of mind and executive control. *Trends in cognitive sciences*, 3(9), 337-344.
- Piaget, J., & Inhelder, B. (1956). *The Child's Conception of Space*. London: Routledge & Kegan Paul.
- Pitskel, N. B., Bolling, D. Z., Hudac, C. M., Lantz, S. D., Minshew, N. J., Vander Wyk, B. C., & Pelphrey, K. A. (2011). Brain mechanisms for processing direct and averted gaze in individuals with autism. *Journal of Autism and Developmental Disorders*, 41(12), 1686-1693.
- Pitskel, N. B., Bolling, D. Z., Kaiser, M. D., Crowley, M. J., & Pelphrey, K. A. (2011). How grossed out are you? The neural bases of emotion regulation from childhood to adolescence. *Developmental cognitive neuroscience*, 1(3), 324-337.
- Power, J. D., Barnes, K. A., Snyder, A. Z., Schlaggar, B. L., & Petersen, S. E. (2012). Spurious but systematic correlations in functional connectivity MRI networks arise from subject motion. *Neuroimage*, 59(3), 2142-2154.
- Preacher, K. J., & Hayes, A. F. (2008). Asymptotic and resampling strategies for assessing and comparing indirect effects in multiple mediator models. *Behavior research methods*, 40(3), 879-891.
- Premack, D., & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *Behavioral and brain sciences*, 1(04), 515-526.
- Pronin, E. (2008). How we see ourselves and how we see others. *Science*, 320(5880), 1177-1180.

Bibliography

- Ramsey, R., Hansen, P., Apperly, I., & Samson, D. (2013). Seeing it my way or your way: Frontoparietal brain areas sustain viewpoint-independent perspective selection processes. *Journal of cognitive neuroscience*, 25(5), 670-684.
- Repacholi, B. M., & Gopnik, A. (1997). Early reasoning about desires: evidence from 14-and 18-month-olds. *Developmental psychology*, 33(1), 12-21.
- Ritter, K., Dziobek, I., Preißler, S., Rüter, A., Vater, A., Fydrich, T., . . . Roepke, S. (2011). Lack of empathy in patients with narcissistic personality disorder. *Psychiatry research*, 187(1), 241-247.
- Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive brain research*, 3(2), 131-141.
- Roberts, J. E., Gotlib, I. H., & Kassel, J. D. (1996). Adult attachment security and symptoms of depression: The mediating roles of dysfunctional attitudes and low self-esteem. *Journal of Personality and Social Psychology*, 70(2), 310-320.
- Rogers, K., Dziobek, I., Hassenstab, J., Wolf, O. T., & Convit, A. (2007). Who cares? Revisiting empathy in Asperger syndrome. *Journal of Autism and Developmental Disorders*, 37(4), 709-715.
- Royzman, E. B., Cassidy, K. W., & Baron, J. (2003). "I know, you know": Epistemic egocentrism in children and adults. *Review of General Psychology*, 7(1), 38-65.
- Santiesteban, I., Banissy, M. J., Catmur, C., & Bird, G. (2012). Enhancing social ability by stimulating right temporoparietal junction. *Current Biology*, 22(23), 2274-2277.
- Santiesteban, I., White, S., Cook, J., Gilbert, S. J., Heyes, C., & Bird, G. (2012). Training social cognition: from imitation to theory of mind. *Cognition*, 122(2), 228-235.
- Satterthwaite, T. D., Elliott, M. A., Gerraty, R. T., Ruparel, K., Loughhead, J., Calkins, M. E., . . . Gur, R. E. (2013). An improved framework for confound regression and filtering for control of motion artifact in the preprocessing of resting-state functional connectivity data. *Neuroimage*, 64, 240-256.

- Saxe, R. (2005). Against simulation: the argument from error. *Trends in cognitive sciences*, 9(4), 174-179.
- Saxe, R., & Kanwisher, N. (2003). People thinking about thinking people: the role of the temporo-parietal junction in “theory of mind”. *Neuroimage*, 19(4), 1835-1842.
- Schmidt, K.-H., & Metzler, P. (1992). *Wortschatztest: WST*: Beltz.
- Schneider, D., Slaughter, V. P., Bayliss, A. P., & Dux, P. E. (2013). A temporally sustained implicit theory of mind deficit in autism spectrum disorders. *Cognition*, 129(2), 410-417.
- Scholz, J., Triantafyllou, C., Whitfield-Gabrieli, S., Brown, E. N., & Saxe, R. (2009). Distinct regions of right temporo-parietal junction are selective for theory of mind and exogenous attention. *PloS one*, 4(3), e4869.
- Schreiter, S., & Pijnenborg, G. (2013). Empathy in adults with clinical or subclinical depressive symptoms. *Journal of affective disorders*, 150(1), 1-16.
- Senju, A. (2012). Spontaneous theory of mind and its absence in autism spectrum disorders. *The Neuroscientist*, 18(2), 108-113.
- Senju, A., Southgate, V., Miura, Y., Matsui, T., Hasegawa, T., Tojo, Y., . . . Csibra, G. (2010). Absence of spontaneous action anticipation by false belief attribution in children with autism spectrum disorder. *Development and psychopathology*, 22(02), 353-360.
- Senju, A., Southgate, V., White, S., & Frith, U. (2009). Mindblind eyes: an absence of spontaneous theory of mind in Asperger syndrome. *Science*, 325(5942), 883-885.
- Shamay-Tsoory, S. G. (2011). The neural bases for empathy. *The Neuroscientist*, 17(1), 18-24.
- Shaw, P., Kabani, N. J., Lerch, J. P., Eckstrand, K., Lenroot, R., Gogtay, N., . . . Rapoport, J. L. (2008). Neurodevelopmental trajectories of the human cerebral cortex. *The Journal of Neuroscience*, 28(14), 3586-3594.

Bibliography

- Siegle, G. J., Thompson, W., Carter, C. S., Steinhauer, S. R., & Thase, M. E. (2007). Increased amygdala and decreased dorsolateral prefrontal BOLD responses in unipolar depression: related and independent features. *Biological psychiatry*, 61(2), 198-209.
- Sifneos, P. E. (1973). The prevalence of 'alexithymic' characteristics in psychosomatic patients. *Psychotherapy and psychosomatics*, 22(2-6), 255-262.
- Silani, G., Bird, G., Brindley, R., Singer, T., Frith, C., & Frith, U. (2008). Levels of emotional awareness and autism: an fMRI study. *Social Neuroscience*, 3(2), 97-112.
- Silani, G., Lamm, C., Ruff, C. C., & Singer, T. (2013). Right Supramarginal Gyrus Is Crucial to Overcome Emotional Egocentricity Bias in Social Judgments. *The Journal of Neuroscience*, 33(39), 15466-15476.
- Singer, T. (2006). The neuronal basis and ontogeny of empathy and mind reading: review of literature and implications for future research. *Neuroscience & Biobehavioral Reviews*, 30(6), 855-863.
- Singer, T. (2012). The past, present and future of social neuroscience: A European perspective. *Neuroimage*, 61(2), 437-449.
- Singer, T., Critchley, H. D., & Preuschoff, K. (2009). A common role of insula in feelings, empathy and uncertainty. *Trends in cognitive sciences*, 13(8), 334-340.
- Singer, T., & Lamm, C. (2009). The social neuroscience of empathy. *Annals of the New York Academy of Sciences*, 1156(1), 81-96.
- Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R. J., & Frith, C. D. (2004). Empathy for pain involves the affective but not sensory components of pain. *Science*, 303(5661), 1157-1162.
- Singer, T., Seymour, B., O'Doherty, J. P., Stephan, K. E., Dolan, R. J., & Frith, C. D. (2006). Empathic neural responses are modulated by the perceived fairness of others. *Nature*, 439(7075), 466-469.

- Small, D. M., Gregory, M. D., Mak, Y. E., Gitelman, D., Mesulam, M., & Parrish, T. (2003). Dissociation of neural representation of intensity and affective valuation in human gustation. *Neuron*, 39(4), 701-711.
- Sommer, M., Döhl, K., Sodian, B., Meinhardt, J., Thoermer, C., & Hajak, G. (2007). Neural correlates of true and false belief reasoning. *Neuroimage*, 35(3), 1378-1384.
- Sommerville, J. A., Bernstein, D. M., & Meltzoff, A. N. (2013). Measuring Beliefs in Centimeters: Private Knowledge Biases Preschoolers' and Adults' Representation of Others' Beliefs. *Child development*, 84(6), 1846-1854.
- Song, X. W., Dong, Z. Y., Long, X. Y., Li, S. F., Zuo, X. N., Zhu, C. Z., . . . Zang, Y. F. (2011). REST: A Toolkit for Resting-State Functional Magnetic Resonance Imaging Data Processing. *PLOS ONE*, 6(9).
DOI 10.1371/journal.pone.0025031
- Sowell, E. R., Peterson, B. S., Thompson, P. M., Welcome, S. E., Henkenius, A. L., & Toga, A. W. (2003). Mapping cortical change across the human life span. *Nature neuroscience*, 6(3), 309-315.
- Spengler, S., von Cramon, D. Y., & Brass, M. (2009). Control of shared representations relies on key processes involved in mental state attribution. *Human brain mapping*, 30(11), 3704-3718.
- Spengler, S., von Cramon, D. Y., & Brass, M. (2010). Resisting motor mimicry: control of imitation involves processes central to social cognition in patients with frontal and temporo-parietal lesions. *Social Neuroscience*, 5(4), 401-416.
- Steinbeis, N., Bernhardt, B. C., & Singer, T. (2012). Impulse control and underlying functions of the left DLPFC mediate age-related and age-independent individual differences in strategic social behavior. *Neuron*, 73(5), 1040-1051.
- Steinbeis, N., Bernhardt, B. C., & Singer, T. (2014). Age-related differences in function and structure of rSMG and reduced functional connectivity with DLPFC explains

Bibliography

- heightened emotional egocentricity bias in childhood. *Social Cognitive and Affective Neuroscience*, nsu057.
- Sterzer, P., Hilgenfeldt, T., Freudenberg, P., Bermpohl, F., & Adli, M. (2011). Access of emotional information to visual awareness in patients with major depressive disorder. *Psychological medicine*, 41(08), 1615-1624.
- Stone, L. A., & Nielson, K. A. (2001). Intact physiological response to arousal with impaired emotional recognition in alexithymia. *Psychotherapy and psychosomatics*, 70(2), 92-102.
- Surtees, A. D., & Apperly, I. A. (2012). Egocentrism and automatic perspective taking in children and adults. *Child development*, 83(2), 452-460.
- Taber-Thomas, B. C., Asp, E. W., Koenigs, M., Sutterer, M., Anderson, S. W., & Tranel, D. (2014). Arrested development: early prefrontal lesions impair the maturation of moral judgement. *Brain*, 137(4), 1254-1261.
- Taylor, G. J., & Bagby, R. M. (2004). New trends in alexithymia research. *Psychotherapy and psychosomatics*, 73(2), 68-77.
- Taylor, G. J., Ryan, D., & Bagby, R. M. (1985). Toward the development of a new self-report alexithymia scale. *Psychotherapy and Psychosomatics*, 44(4), 191-199.
- Thoma, P., Zalewski, I., von Reventlow, H. G., Norra, C., Juckel, G., & Daum, I. (2011). Cognitive and affective empathy in depression linked to executive control. *Psychiatry research*, 189(3), 373-378.
- Thomas, R. C., & Jacoby, L. L. (2012). Diminishing adult egocentrism when estimating what others know. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 39(2), 473-486.
- Thompson, L., & Loewenstein, G. (1992). Egocentric interpretations of fairness and interpersonal conflict. *Organizational Behavior and Human Decision Processes*, 51(2), 176-197.

- Tops, M., Riese, H., Oldehinkel, A. J., Rijdsdijk, F. V., & Ormel, J. (2008). Rejection sensitivity relates to hypocortisolism and depressed mood state in young women. *Psychoneuroendocrinology*, 33(5), 551-559.
- Tottenham, N., Tanaka, J. W., Leon, A. C., McCarry, T., Nurse, M., Hare, T. A., . . . Nelson, C. (2009). The NimStim set of facial expressions: judgments from untrained research participants. *Psychiatry research*, 168(3), 242-249.
- Twenge, J. M., Miller, J. D., & Campbell, W. K. (2014). The narcissism epidemic: Commentary on Modernity and narcissistic personality disorder.
- Van Boven, L., & Loewenstein, G. (2003). Social projection of transient drive states. *Personality and Social Psychology Bulletin*, 29(9), 1159-1168.
- Van Overwalle, F. (2009). Social cognition and the brain: A meta - analysis. *Human brain mapping*, 30(3), 829-858.
- Waring, J. D., Etkin, A., Hallmayer, J. F., & O'Hara, R. (2013). Connectivity Underlying Emotion Conflict Regulation in Older Adults with 5-HTTLPR Short Allele: A Preliminary Investigation. *The American journal of geriatric psychiatry: official journal of the American Association for Geriatric Psychiatry*, 22, 946–950.
- Washington, S. D., Gordon, E. M., Brar, J., Warburton, S., Sawyer, A. T., Wolfe, A., . . . Mbwana, J. (2013). Dysmaturation of the default mode network in autism. *Human brain mapping*, 35(4), 1284-1296.
- Wellman, H. M., Cross, D., & Watson, J. (2001). Meta - analysis of theory - of - mind development: the truth about false belief. *Child development*, 72(3), 655-684.
- Wigfield, A., & Guthrie, J. T. (1997). Relations of children's motivation for reading to the amount and breadth of their reading. *Journal of educational psychology*, 89(3), 420.
- Wilbertz, G., Brakemeier, E.-L., Zobel, I., Härter, M., & Schramm, E. (2010). Exploring preoperational features in chronic depression. *Journal of affective disorders*, 124(3), 262-269.

Bibliography

- Williams, B. R., Ponsesse, J. S., Schachar, R. J., Logan, G. D., & Tannock, R. (1999). Development of inhibitory control across the life span. *Developmental psychology*, 35(1), 205-213.
- Wimmer, H., & Perner, J. (1983). Beliefs about beliefs: Representation and constraining function of wrong beliefs in young children's understanding of deception. *Cognition*, 13(1), 103-128.
- Wittchen, H.-U., Wunderlich, U., Gruschwitz, S., & Zaudig, M. (1997). Skid-i. *Strukturiertes Klinisches Interview für DSM-IV*.
- Wolkenstein, L., Schönenberg, M., Schirm, E., & Hautzinger, M. (2011). I can see what you feel, but I can't deal with it: Impaired theory of mind in depression. *Journal of affective disorders*, 132(1), 104-111.
- Wolkenstein, L., Zeiller, M., Kanske, P., & Plewnia, C. (2014). Induction of a depression-like negativity bias by cathodal transcranial direct current stimulation. *Cortex*, 59, 103-112.
- Zobel, I., Werden, D., Linster, H., Dykieriek, P., Drieling, T., Berger, M., & Schramm, E. (2010). Theory of mind deficits in chronically depressed patients. *Depression and Anxiety*, 27(9), 821-828.

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List of Abbreviations

ACC	Anterior Cingulate Cortex
ADI-R	Autism Diagnostic Interview - Revised
ADOS	Autism Diagnostic Observation Schedule
AI	Anterior Insula
ANCOVA	Analysis of Covariance
ANOVA	Analysis of Variance
ASD	Autism Spectrum Disorder
BDI	Beck Depression Inventory
dACC	dorsal Anterior Cingulate Cortex
DIPFC	Dorsolateral prefrontal cortex
DSM	Diagnostic and Statistical Manual of Mental Disorders
EEB	Emotional Egocentricity Bias
ETAP	EEB Taste –Paradigm
EMOP	EEB Money Game –Paradigm
ETOP	EEB Touch –Paradigm
HAMD	Hamilton Depression Scale
HAWIE-R	Hamburg-Wechsler-Intelligenztest für Erwachsene
HC	Healthy Controls
IFG	Inferior Frontal Gyrus
IPL	Inferior Parietal Lobule
IRI	Interpersonal Reactivity Index
fMRI	functional Magnetic Resonance Imaging
KCl	Kaliumchlorid

IDL PFC	left Dorsolateral Prefrontal Cortex
LMS	Labeled Magnitude Scale
lSMG	left supramarginal gyrus
lTPJ	left temporo-parietal junction
M	Mol
MASC	Movie for the Assessment of Social Cognition
MCC	Middle Cingulate Cortex
MDD	Major Depressive Disorder
mM	Millimol
MPFC	medial prefrontal cortex
NaCl	Natriumchlorid
NaHCO₃	Natriumhydrogencarbonat
PCC	Posterior Cingulate Cortex
RMITE	Reading the Mind In The Eyes test
rSMG	right supramarginal gyrus
RT	Reaction Times
rTPJ	right temporo-parietal junction
SCID	Structured Clinical Interview for DSM Disorders
SMG	Supramarginal Gyrus
tDCS	transcranial current stimulation
ToM	Theory of Mind
TPJ	Temporo-parietal Junction
WST	Wortschatztest

Selbständigkeitserklärung

Hiermit erkläre ich, dass die vorliegende Arbeit ohne unzulässige Hilfe und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt wurde und dass die aus fremden Quellen direkt oder indirekt übernommenen Gedanken in der Arbeit als solche kenntlich gemacht worden sind.

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